A STUDY OF SOME ASPECTS OF HONEYBEE NUTRITION IN THE SOUTH-EAST OF SCOTLAND WITH SPECIAL REFERENCE TO POLLEN

by

Archibald Robertson McLellan

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SUMMARY

Colonies of honeybees gather and consume pollen and nectar; the pattern of collection of these substances, certain aspects of their composition, the individual pollen types utilised and the effect of variations in the pattern of nectar collection on colony development have been investigated in the South-East of Scotland. A very small proportion of the available flora is utilised by bees for pollen gathering and an even smaller number of pollen types are collected in any quantity. The mean active pollen gathering period is only between 107 and 120 days long. Variability between colonies rather than between sites accounted for most of the differences between the amounts of pollen trapped. Most pollen and most pollen types were gathered when brood rearing was at its peak. Mixed woodland was the habitat from which bees gathered relatively most pollen and sycamore was the best individual source; less pollen was collected from meadowland and arable land; in the former white clover was the best source and cruciferous weeds in the latter. The same pollen types were harvested from the one site during the 4 years in which it was investigated although individual colonies there showed slightly different preferences.

Trapping pollen from colonies did not affect the amount of brood reared although it appeared to influence the winter survival and also produced a few other temporary effects. A variable proportion of the total pollen being harvested

appeared to be culled from the colonies throughout the active season by the traps.

Significant relationships between the colony weight and the amount of honey in store throughout the active season ($r = 0.94$) allowed a study of the nectar flows in the area to be made by direct weighing of the colonies in their hives. This established that good nectar flows occurred on the Lothians' coast in early summer and in the upland area to the south of this coast in mid and late summer. The first of these produced transient effects upon the colonies while the second affected the amount of honey stored (36 kg stored in upland colonies compared with 11 kg in the coastal ones) and the brood reared.

All the colony characteristics measured with the exception of honey in store reached their maxima about mid-summer when they averaged 37,000 adult bees, 2.7 kg stored pollen and 21,000 brood. Larger colonies stored most honey by the end of the season and reared most brood; but the only significant correlations were those between the pollen trapped per day and the brood, and between the mean pollen in store and the brood.

As a result of chemical investigations the results mentioned in this next section seemed most worthy of note. Fresh pollen contained 27% water. Wooden traps produced pollen in a much more satisfactory state than metal ones. The mean lipid and ash content of the pollens was low. About 31% of the pollen consisted of sugars, which are valu-

able food materials for honeybees. The gross energy of pollen was high (5,500 kilo calories per g). Pollens contain a low quantity of nucleic acid. Most of the nitrogen content of pollens after hydrolysis was in the form of amino acids. The various types of pollen showed a close similarity in the relative amounts of amino acids which they contained with the exceptions of serine, cystine and histidine. Analyses of honeybee carcasses indicated that their amino acid contents were very similar to those of the pollens which are therefore nearly ideal sources of these nutrients for bees. Pollens were also found to be better sources of the minerals Na, Mg, K and P for honeybees than honey in which the cation pair K and Mg were closely related, and Mg was most affected by the other ions investigated.

PLATE and FIGURES

I INTRODUCTION

In 1970 the honey produced by the beekeepers of Scotland was worth, retail, about half a million pounds sterling. This rate of production cannot satisfy consumer demand and as a consequence much imported honey is sold. The production of more honey depends upon several factors. One of the most important of these is the environment in which the colonies are situated. There is at the moment no method of accurately assessing areas for their beekeeping potential other than by the use of trial-and-error methods. Detailed studies of the exploitation of these areas by honeybees are few in number. Although the main pollen and nectar plants are known, the relative amounts of foodstuffs that are required for the colony development and honey production are as yet imprecisely understood. It is, therefore, important that areas should be studies in detail in order to understand the intricate relationships between the flora and the honeybee.

Once the production factors are determined by careful monitoring of the pollen and nectar income and their effects upon the colonies, the relative importance of the different parts of the environment can be assessed. This information can then be used to forecast the potential production of different areas for beekeeping, and the time when this harvest will be gathered, so that management can be modified accordingly.

Of all the foodstuffs utilised by the honeybee (*Apis mellifera* L.) pollen is the predominant source of proteins,

fats, minerals, vitamins and amino acids for honeybees. Pollen is also the basic food for rearing the larval honeybees, feeding the laying queen, developing the hypopharyngeal glands that produce some of the larval food, and for maintaining the normal protein balance in older honeybees (Herbert, et al., 1970). The pollen supply is therefore one of the most important factors in the life of a honeybee colony and a chemical examination of the composition of the pollens gathered by honeybees in any habitat is fundamental in assessing their nutritional potential in any study of the honeybee economy. Chemical analyses, although not indicating either the digestibility or availability of nutrients in foodstuffs, do indicate their relative abundance and are fundamental in the assessment of food materials. Furthermore the chemical composition of pollen from different species of plants varies widely and thus the total amount gathered in any locality may not be used as a true index of the actual food value of the pollen (Eckert, 1942). It is hoped that from this and similar studies, a sound assessment of the nutritive potential of pollens will be compiled and that this knowledge will aid in the construction of an artificial diet for honeybees. Such a diet would have great practical value to commercial beekeepers engaged in producing honey, package bees or queen honeybees and in addition would be useful in experimental investigations of the nutrition of phytophagous insects in general and the honeybee in particular.

II REVIEW OF LITERATURE

II.1 Pollen-gathering by honeybees

General factors

The gathering instinct is well defined in the honeybee, Louveaux (1958) compared it to the hoarding instinct of the rat. This particular behaviour is capable of some modification, for example, not only does the gathering pattern differ in colonies of different strength (Todd and Bishop, 1940), but the amount of brood present in a colony affects the pollen harvest (Louveaux, 1958, Todd and Bishop, 1940, Free, 1967). The genetic constitution of the honeybee also appears to affect the pollen harvest (Louveaux, 1958) and the loss of the queen can reduce the amount of pollen gathered (Louveaux, 1958).

The local flora is also important because, if no flowers are in bloom at any time, no pollen can be gathered. Climate is another important factor affecting the flight of honeybees and influencing the presentation of pollen by flowers.

Climatic and floral factors

Variations in the weather can affect the honeybee directly, and indirectly by their effects upon the flowering plant. The flight activity of the honeybee normally ceases when the air temperature falls below 8-10°C (Wilson, 1922; Bodenheimer and Ben Nerya, 1937); while an increase in light intensity tends to stimulate bee flight (Butler and

Finney, 1942). An increase in wind velocity or precipitation on the other hand decreases flight activity (Ribbands, 1953). The relationship between pollen collecting and weather has been examined by Rashad and Parker (1958a) and Todd and Bishop (1940) have stated that climatic effects are not so marked on larger colonies. Climate can also affect flowers, the actual flowering period being advanced or retarded by the weather (Jeffree, 1958b) and the time of pollen release by the dehiscence of the anthers is affected by the temperature, relative humidity and time of day (Percival, 1965).

The influence of local environmental factors on the types of pollen harvested by honeybees

Some believe that the pollens gathered by honeybees are mostly from the wild flower species common in that particular neighbourhood (Percival, 1947), while others claim that most pollens are harvested from cultivated plants like rape (Brassica napus), clovers (Trifolium spp.) and the weeds associated with the disturbed ground conditions of agriculture (Schwan and Martinovs, 1954). Others believe that different flowers are utilised in different areas for pollen collecting (Todd and Bishop, 1940, 1944; Maurizio and Kollmann, 1949) and Louveaux (1958) claimed that a country could be divided into several major ecological areas for pollen harvesting, each area being typified by its own pollen types.

Number of pollen types harvested

Although Parker (1926) was one of the earliest investigators to study honeybees collecting pollen, Andrewjew (1928) first reported that honeybees gathered relatively few species from the local flora. In studying the total number of plant species worked by honeybees at Camberley in the South of England, Betts (1928, 1935) confirmed Andrewjew's observation but produced no data on the relative amounts gathered. Stapel and Eriksen (1939) studied the flora used by honeybees in a district of Denmark and found that most of the pollen was produced from a restricted part of the total flora. A study of pollen collection in different areas of California (Todd and Bishop 1940, 1944) showed large variations in the amount of pollen harvested in different areas, and even by colonies in the same apiary, but nothing was reported about the pollen species gathered. In her study of the pollen trapped at Rothamsted over 2 years, Synge (1947) stated that over 60% of the pollen was derived from legumes and rosaceous plants. Percival (1947) working on a colony near Cardiff confirmed that relatively few species of flowers were exploited for pollen in quantity by honeybees. Jaxtheimer (1949), working in Munich, reported similar results and added that the flowers visited more, were those which occurred more frequently in the neighbourhood of the colony. Hare and Vansell (1946), trapping pollen only during the flowering period of the alfalfa, found that 75% of the total pollen was from two

plant species. Harris and Filmer (1948) in New Zealand also reported a similar state of affairs with about 70% of their harvest from lupins, thistles and clover.

Pollen preferences

Eckert (1942) observed that different colonies in the same apiary had their own pollen preferences and Synge (1947), Schwan and Martinovs (1954), Maurizio (1953) and Louveaux (1958), stated that such differences could be noted even in closely related colonies, and Louveaux added that this was really a phenomenon of preference for particular floral families rather than individual species. He observed that some colonies collected very few species of pollen while others were not quite so restricted in their collecting activity. Eckert (1942) had already noted that when many pollens were encountered in the pollen loads of the returning foragers it was a sign of pollen scarcity. Jaxheimer (1949) on the other hand claimed that although daily harvests of pollen might differ in neighbouring colonies when trapping began at the beginning of the season such differences became very small after about one month.

Many theories have been proposed to account for the choice of pollen types by honeybees. Lavie and Fresnaye (1963) said that bees selected the most nutritious pollen. Louveaux (1958) claimed that factors like powderiness and the presence of chemical attractants as well as the nutritional value were perhaps important. Louveaux also reported a nitrogen cycle in the pollens gathered which reached its

maximum in the May-June period, while Robinson and Nation (1968b) reported that an acetone soluble portion of the pollen increased the attractiveness to honeybees of any foodstuff to which it was added.

Pollen trapped

The weights of pollen trapped from colonies of honeybees in one season vary considerably. Todd and Bishop (1940) reported annual amounts ranging from 8 to 18 kg for different parts of California. Eckert (1942) also working in California, but shifting pollen traps from colony to colony frequently, claimed that between 50 and 55 kg were harvested annually from colonies. Synge (1947) in the U.K. reported harvests of between 1.4 and 1.5 kg (during a bad season) and Hirschfelder (1951) in Germany between 2.3 and 9.1 kg, while Louveaux (1958) in France stated that the average amount trapped was between 2.3 and 3.3 kg. Much of this variability can be attributed to different methods of trapping (Eckert, 1942) different traps (Hirschfelder, 1951) and different locations (Todd and Bishop, 1940).

The amount of pollen collected by colonies of honeybees in one season

Various estimates of this have been made based upon trapping returns, or the amount of pollen required to rear a certain quantity of brood. Todd and Bishop (1940) for example, calculated that between 20 and 30 kg of pollen were required to rear the 200,000 bees that Nolan (1925)

claimed were produced by a colony in one season. Schaefer and Farrar (1941) reduced this to between 18 and 23 kg and Synge (1947) calculated, on the basis of trap returns that her colonies collected between 5.6 and 5.9 kg in a bad season. Hirschfelder (1951) using similar methods to Synge estimated that between 17 and 27 kg were gathered by colonies in one season and Louveaux (1958) stated that 23 to 33 kg pollen were gathered by the majority of his colonies on the basis of trap returns.

Pollen and nectar gathering

The proportion of pollen loads to nectar loads taken into a hive varies widely, being largely dependent upon both available forage and colony requirements. In good nectar flows, the proportion of pollen gatherers and the total quantity of pollen brought in may not diminish, but the proportion of pollen to nectar loads falls off very quickly, because the nectar gatherers complete their trips more quickly (Ribbands, 1953). This implies that within the colony environment, pollen and nectar gathering tend to be two separate processes. Pollen and nectar can be produced from separate plant species, and even among plants yielding both nectar and pollen the proportion of the two foods collected at any time depends upon their relative availability, for if the nectar supply decreases as the day progresses this may induce increased pollen collection without any change in pollen availability (Ribbands, 1953). Foraging honeybees have been observed to prefer nectar to

pollen crops (Ribbands, 1949) although Singh (1950) did on one occasion notice the opposite. Louveaux (1958) has however claimed that pollen and nectar gathering by colonies of honeybees are unrelated processes.

The weights of pollen loads

Each pollen load consists of two pellets and according to Gillette (1897) the weight of a pollen load is about 11 mg. Park (1922) stated that the pollen load varied with the species of flower and ranged from 11 to 29 mg and could vary with densities of pollen. Parker (1926) quoted an average pollen load of 15 mg and Maurizio (1953) weighed different species of pellets and reported that the weight of average loads of pollen ranged from 8.4 to 22 mg. According to this evidence, the average pollen load of a foraging honeybee weighs about 15 mg but could vary from 8.4 to 29 mg.

Mixed pollen loads

This phenomenon has been observed and discussed by Betts (1935), Percival (1947), Maurizio (1953) and Free (1963) who were all of the opinion that pollen pellets were mostly homogeneous and true mixtures constituted only a very small percentage of the total pollen carried into the hive.

The foraging range of honeybees

Beutler (1954) claimed that the foraging range for pollen around a beehive was almost 500 metres, while

Percival (1947) stated that ¼ mile, (about 400 m) was the normal foraging limit for pollen-foraging honeybees. Ribbands (1949) reported that pollen loads were gathered much more rapidly than nectar loads and so concluded that the economic flight range for pollen gathering was less than for nectar. Ribbands (1951) reported that reductions in nectar collection due to increasing distance between the colony and the nectar source were detectable, in some instances this effect was noticed from about 650 metres, varying according to the weather and being most marked on days of low temperature, high winds and little sunshine, although it varied to some extent also according to the number of bees in the colony (Todd and Bishop, 1940).

The relationship of pollen to other factors in the honeybee colony

In any study of the development of colonies of honeybees it is important to make observations on the quantities of adult honeybees, brood, honey and pollen which are apparently the most important factors within the colony. These variates are all subject to annual fluctuations which are particularly marked during the active season and in any study concerned with any one of these factors, for example, pollen, careful observations of the other factors are necessary if the inter-relationships are to be understood.

However, although systematic records of one or two of these factors have been made from time to time, few workers have attempted to measure all these variables simultaneously

despite their importance, or to attempt to interpret their inter-relationships.

The numbers of adult bees during the year have been measured by Farrar (1931) in the United States and Jeffree (1955) in the United Kingdom, while the amount of brood present during the summer has been described by Nolan (1925) and Allen (1965b) and during the winter by Jeffree (1956). Mitchener (1947, 1955), Kettner (1961) and others have indicated the amount of honey stored in the summer from the results of hive weighings and the amount of pollen harvested has been examined by Todd and Bishop (1940, 1941), Synge (1947), Hirschfelder (1951) and others. Pollen stored has been studied by Jeffree and Allen (1957). A few attempts have been made to relate two or more of these variables together (Ribbands, 1953; Allen and Jeffree, 1956; Rashad and Parker, 1958a,b), but no clear picture of the connection between these variables has emerged. This present study was undertaken in an attempt to clarify these complex inter-relationships.

II.2 Pollen Traps

Pollen trapping

The determination of the relative amount of different pollen types collected by colonies of honeybees in specific areas is not easily accomplished. There are two methods of dealing with the problem. One is by hand-trapping the bees and removing their pollen loads as they return to the

hive entrance from foraging. This is time-consuming; only one colony can be dealt with at one time and only a small percentage of the loads can be collected. It can, however, be useful as was shown by Betts (1928) who did some of the pioneer work. The weakness of this method is that human observers cannot count quickly and accurately enough to deal with the very active colonies of honeybees, and in the selection and removal of pellets there may be a tendency to remove only certain types.

The other method involves the use of traps which are made in such a way that the bees entering and leaving the hive have to pass through a wire grid or perforated screen at the hive entrance and in doing so the screen may remove one or both of the pollen pellets which the honeybees are carrying. It was assumed by some observers that this device would remove a fixed percentage of the pollen loads entering the hive (Free, 1967). The traps can be left unattended for several days, and still remain functional. In addition, more pollen can be collected, and in a more objective manner than by hand methods, and several colonies can be studied at the same time. However although pollen traps like all sampling devices such as pitfall traps, sweep nets, and Berlese funnels have their limitations they can be valuable in obtaining fairly large quantities of pollen from colonies of honeybees.

The development of pollen traps

Apparently the first pollen trap was devised by Eckert (Eckert and Shaw, 1960) in 1927 in order to study the flora utilised by honeybees at a site in Wyoming, U.S.A. Prior to this period queen excluders had been used to reduce the pollen intake by colonies situated in areas where it was thought that excess pollen was being gathered and stored (Herrod-Hempsall, 1930). One of the first pollen traps to be described in detail in the literature was the one of Farrar (1934). It was called a 'pollen guard' and was employed to remove the pollen from incoming honeybees so that the effects of pollen deprivation might be studied. Basically, this trap consisted of two metal sheets, each perforated by 44 holes of 3/16" diameter (about 5 mm). These holes were designed to allow bees into the hive but to remove the pollen which they carried. The whole unit was enclosed in a wooden storm shield to exclude rain. Schaefer and Farrar (1941) found it more convenient to replace the perforated metal sheet by wire cloth and Synge (1947) used a modified form of the latter trap for studying the pollens obtained around Rothamsted.

On the continent of Europe, Böttcher (1941, 1943) described a pollen trap constructed from perforated sheets of celluloid. This device appears to be related to the earlier American sheet metal traps (Budel and Herold, 1960). Like most continental traps that of Böttcher had little slots radiating from the main holes for the bees' legs to

pass through. Maurizio and Killmann (1949) and Hirschfelder (1951) apparently used traps of this type successfully. Recently other modified traps have been used by Rashad (1957), Louveaux (1958) and Lavie and Fresnaye (1963).

The effect of pollen traps upon colonies of honeybees

According to Eckert (1942) and Lindauer (1952) honeybee colonies adjust themselves to pollen traps by gathering more pollen. Honeybees, can only compensate to a certain extent for the presence of pollen traps, because if too much pollen from the harvest were removed by the trap the colony would decline (Eckert, 1942).

Hirschfelder (1951) stated that this extra pollen was gathered at the expense of honey harvesting and claimed that 250 g of honey was lost per kg of pollen gathered, while Rashad (1957) said that pollen traps placed on colonies of honeybees increased the pollen collection by 80% and reduced the honey production by 41%. Rybakov (1961) did not agree with these figures and stated that traps actually increased the honey gathered from 35 to 41 kg per colony. Lindauer (1952) demonstrated that on colonies fitted with traps a greater proportion of the foragers were pollen harvesters; this was in agreement with Hirschfelder (1951) and Rashad (1957).

Colonies of honeybees thus apparently compensate for the removal of some of the pollen by increasing the number of foragers gathering pollen but compensation cannot take

place indefinitely without loss of honey.

The efficiency of pollen traps

Various assessments of pollen-trap efficiencies have been made. Synge (1947) counted the number of pellets collected in a given time by a trap with 2 grids and compared this with the number of pellets seen entering the hive. Eight such counts were made giving an average of 25.3% ± 0.78 for the amount of pollen caught by the trap. Free (1959, 1965), who used a single grid type of this trap and a similar method of assessment stated that it removed about 10% of the pollen load from returning foragers. Louveaux (1958) used a similar trap but with 2 grids and claimed that it had a 10% ± 5 efficiency. A Bottcher pattern trap was stated to be 10% efficient (Maurizio and Kollmann, 1949). The pollen trap is not a perfect tool. Limitations were described by Free (1965) who said that they produced "comparative information on the amounts of pollen collected by different colonies". He added that the information obtained was not necessarily completely accurate because "large loads are more likely to be removed by pollen traps". Nevertheless, workers have felt sufficiently confident to use them for estimating the relative amounts of pollen collected by colonies of honeybees.

II.3 Nectar flows

Honeybee colony weight and honey stored

Colonies of honeybees weighed regularly throughout the

active season are very useful indicators of honey flows (Morland, 1929; Mitchener, 1947; Oertel, 1950). They can therefore be used to investigate the conditions favouring honey production provided the weighed colonies are manipulated in a similar manner to the others (Oertel, 1950). In spite of these claims, there have been apparently no detailed examinations of the relationship between hive weight and nectar flows apart from that of Wafa (1954) nor have weighing machines been much used in beekeeping practice outside Switzerland (Eberhard, 1947) or certain parts of Germany (Kettner, 1961) and North America (Parkes, 1927; Mitchener 1947) probably because of the expense of suitable machines. An example of what can be done by their use is given by Mitchener (1955) who showed how they could be used to determine the best times for establishing and destroying package colonies of honeybees.

The effects of nectar flows on colonies of honeybees

Attempts to simulate the effect of nectar flows on colonies of honeybees by feeding sugar syrup have been carried out by various workers (Butler, 1946; Crane, 1950; Ribbands, 1950) and especially by Free and Spencer-Booth (1961). The failure to produce an increase in brood rearing when sugar syrup was fed during good weather conditions suggested to the last two investigators that this lack of response was caused by the availability of natural food. Thus it appears that the use of artificial nectar flows cannot replace field experiments in which the effect of natural flows upon colonies of honeybees are examined.

II.4 Chemical aspects of pollen composition

Introduction

Pollen is an essential substance for various insects particularly bees, because it is the source of most, if not all, of the nitrogenous material in adult and larval nutrition. In spite of the obvious importance of pollen in nature little detailed analysis has been carried out mainly because of the difficulty of gathering sufficient pollen. Hügel (1962) summarised the situation thus "The literature of pollen chemistry is relatively poor, the analyses are few, and where a number of constituents have been isolated few have been identified".

The water content of pollen

Estimations of the water present in pollen are important because they indicate the amount of water the honeybee is obtaining from this source and also because they indicate the relative amount of dry matter, containing nutrients, that is present in the pollen. Nevertheless there are no reports of this constituent in the otherwise fairly comprehensive reviews of pollen literature by Parker (1926), Lunden (1954) and Hügel (1962). The mean water content of four mixed pollens trapped from honeybees and reported by Vivino and Palmer (1944) as 23.89 $\pm$ 0.88% is one of the few available. Other authors tend to report only the water content of the crude air-dried pollen (Todd and Bretherick, 1942), the pollen fresh weight

(Eckert, 1942) or the number of pollen pellets harvested (Percival, 1947).

Carbohydrates

As honey is the major source of carbohydrate for honeybees the interest shown in pollen carbohydrates has been small. Analyses show that pollens are rich in carbohydrates but as Todd and Bretherick (1942) indicated, the mode of collecting the pollens must be considered when judging the analytical results. Bee-collected pollens always contain large amounts of sugars due in part to the presence of honey or nectar in the fluid cementing the grains together. In addition, if pollens are left for any time in a moist condition enzymic breakdown may result, decreasing the amount of non-reducing sugars. On the other hand, pollens which have been mechanically collected and air-dried tend to be poor in reducing and rich in non-reducing sugars. Sugar analyses have been reported by von Planta (1885) and Anderson and Kulp (1922) for different species of pollens, and indicated that between 8 and 19% of the dry matter of the pollens examined consisted of pentoses and other reducing sugars in addition to sucrose. The investigations of Todd and Bretherick (1942) on over 30 species of pollens showed a range of reducing sugar values from 20 to 40% of the dry matter in honeybee-collected material and from 0 to 7.5% of the dry matter for 6 hand-collected samples of different species of pollens. The corresponding figures for non-reducing sugars were 0 to 9%

of the dry matter respectively.

Since that time von Euler et al (1945) have isolated ribose and deoxyribose from pollens, and Khun and Low (1949) have demonstrated the presence of lactose in forsythia pollens; this was the first time lactose had been detected with certainty in material of plant origin. In further work, with paper chromatography, Weygand and Hoffmann (1950) determined the contents of glucose and fructose, sucrose, raffinose and stachyose in pollen extracts. More recently the sugars of pollen grains have been examined by Motomura et al (1962) and Schanderl et al (1963) who stated that fructose, glucose and sucrose are the commonest sugars in pollens. Polysaccharides such as pentosans, starch and cellulose have also been detected in certain pollens (von Planta, 1885; Anderson and Kulp, 1922). Todd and Bretherick (1942) detected starch in all but 3 of the pollen species examined, the highest quantity (22%) being obtained from maize.

Carbohydrates have often been detected in protein-containing pollen extracts; in most cases however quantitative analyses have not been attempted. Robbins et al (1948) did produce values for the total carbohydrate and pentose fraction that produced an allergic reaction on human skin.

Proteins

Since pollens are the major source of amino acids for honeybees, a thorough knowledge of the amino acid composition

of pollens is of great importance in honeybee nutrition. The total amount of crude protein in pollens has been examined by von Planta (1885), Todd and Bretherick (1942) and Vivino and Palmer (1944). The crude protein contents vary considerably ranging from 11 to 35% of the dry matter (Todd and Bretherick, 1942). It has been claimed (Hügel, 1962) that honeybees often prefer pollens that are rich in protein, but Lunden (1954) stated that there was no special preference among bees for pollens of high protein value, though pine pollens which were unusually low in protein were only occasionally collected by honeybees (Todd and Bretherick, 1942). Sipe (1923) using histological methods claimed that most of the protein of pollens was located in the dense non-vaccuolated protoplasm inside the pollen grain where presumably it acted as a reserve foodstuff.

The protein fractions of pollens have mostly been studied by allergists who have attempted to separate the various proteins by the techniques of electrophoresis, ultracentrifugation and diffusion in attempts to isolate and identify the agents thought to cause pollen allergies. Much of this work has been performed on the ragweeds (Artemisia elatior and A. trifida) of the U.S.A. and various workers have succeeded in determining that the allergic activity is most intense in a low molecular weight fraction (M. Wt. about 5,000) containing both protein and carbohydrate (Abramson, 1947). Since then the chemical constituents of these allergens have been analysed more intensively

(Linskens, 1961). Little appears to be known of the proteins of pollen species of no special interest to allergists.

Amino acids

Although some amino acids had been identified in pollens before the development of partition chromatography, little work of real significance had been performed. The first systematic study of the amino acids in pollens collected by honeybees was the semi-quantitative examination by Auclair and Jamieson (1948) using paper chromatography. These results indicated that all the common amino acids were present in pollen, either bound in protein or in the free state. The amino acids considered to be essential for growth (Groot, 1952), were invariably present except phenylalanine and tryptophan. The former was found to be missing in dandelion (Taraxacum officinale), willow (Salix spp.) and a mixed pollen while tryptophan could not be detected in dandelion pollen. Vivino and Palmer (1944) obtained indication of a tryptophan and methionine or cystine deficiency in feeding a mixed bee-collected pollen to rats.

Quantitative analyses of pollens using microbiological methods have been reported by Weaver and Kuiken (1951) who determined the essential amino acids of willow, (Salix spp.), larkspur (Delphinium virescens), post oak (Quercus stellata), bluebonnet (Lupinus texensis), partridge pea (Cassia fasciculata) and a mixed pollen and also by Sarkar et al. (1949) in the analysis of sweet corn (Zea mays) amino acids.

Although the crude protein values for the different pollens were found to vary considerably (range 19.7 to 33.3% of the dry matter), the percentages of essential amino acids in the protein showed only slight variations. When the essential amino acid content of the pollens was compared with that of 3 different proteins of high nutritional value from soya bean (Glycine max), flour, casein, and whole egg, which were often used as the basis for the formulation of artificial pollens, it was apparent that no great differences existed.

A comparison between the amino acid composition of leaves and pollen was carried out by Virtanen and Kari (1955). They found that pollen contained more proline and pipecolic acid than leaves but less citrulline.

Lipids

Lipids are usually extracted from materials by the ether extraction procedure which produces a mixture of 'fatty' or 'oily' substances. Hazel (Corylus avellana) pollen was one of the first to be examined (von Planta, 1885); over 4% of its dry matter was found to be 'fat'. Since then other lipid determinations have been made (Koessler, 1918; Anderson and Kulp, 1922; Todd and Bretherick, 1942; Vivino and Palmer, 1944; Virtanen and Kari, 1955). The amount of ether extractable material in these pollens showed a wide variation with values ranging from about 1 to 20%. In their extensive investigation of different pollen species, Todd and Bretherick (1942) reported a mean value of about 5%

for air dried, bee-collected pollens. The maximum values were obtained from dandelion, 14%, and some mustard species, 8 to 13%.

Little is known of the lipids required by larval honeybees although it would appear that they are necessary for successful pupation (Petit, 1963); apparently adult honeybees do not require lipids (Haydak and Dietz, 1965). However there appear to be lipid materials in pollen which are highly attractive to honeybees and increase their food consumption (Robinson and Nation, 1968b).

Many diverse compounds have been isolated or identified in these pollen lipid mixtures. In corn pollens, Anderson (1923) isolated a nonacosane, a saturated C_{30} alcohol, a phosphatide and the palmitic acid ester of a sterol. When studying hazel pollens, Sosa and Sosa-Bourdouil (1952) found about 15% was lipid containing fatty acids, 5%, non-saponifiable material, 2.6%, hydrocarbons, 0.6%, and sterols, 0.6%, while Nilsson et al. (1957) using spectrography identified the paraffins, n-tri, n-penta, n-hepta and n-nonacosane in the acid fraction of the lipid extract after saponification. Barbier et al. (1960) and Hügel (1962) isolated 24-methylene-cholesterol from pollens. The latter claimed that this chemical was perhaps the attractant for honeybees in pollen and also that it was probably one of their main sources of sterol. Since then Hügel et al. (1964) have isolated several other sterols from pollens.

Pigments

The wide variety of colours found in different pollens are mainly due to flavanol and carotenoid compounds. Colours range from dark blue, rosebay willowherb (Chamaenerion angustifolium) and vipers bugloss (Echium vulgare); green, meadow sweet (Filipendula ulmaria); light pinkish white, heaths (Ericaceae); with yellows (Cruciferae) and pale browns, white clover, (Trifolium repens) being particularly common. These differences are often useful in helping to separate the pollen types.

Minerals

The ash content of different pollen species has been examined by von Planta (1885), Todd and Bretherick (1942) and Vivino and Palmer (1944). The mean value of ash in different pollens was about 3% but ranged from 1 to 7%. The composition of the pollen ash was quantitatively determined by several workers. It consisted mainly of potassium, 20 to 45%; magnesium, 1 to 12%; calcium, 1 to 15%; phosphorus, 1 to 20% (Anderson and Kulp, 1922; Todd and Bretherick, 1942; Vivino and Palmer, 1944). Silicon was found in quantities between 2 and 10% of the total ash (Anderson and Kulp, 1922).

Enzymes

Pollen carries the chromosomal compliment from one parent and associated with its reproductive function is the growth of a special tube down the pistil of the 'mother plant'. To carry out this function the pollen must contain

several enzymes in addition to the respiratory ones associated with the normal metabolic processes. Several of these enzymes have been examined in connection with studies of pollen chemistry. The respiratory enzymes have been investigated by Okonuki (1951a) as have the glycolytic enzymes (Okonuki, 1951b), while Palumbo (1953) has examined several phosphatases and more recently Gherardini and Healey (1969) claimed to have identified the enzymes which degrade the angiosperm pollen grain wall during germination.

Vitamins

Since the discovery of the curative effect of corn pollen on avian polyneuritis (Dutcher, 1918) a few workers have examined the vitamin content of pollens. Angiosperm pollens are unusually rich in water soluble vitamins (Anderson and Kulp, 1922; Haydak and Palmer, 1940; Vivino and Palmer, 1944; Nilsson et al. 1957); the thiamine, riboflavin, pantothenic acid, nicotinic acid and ascorbic acid are as high or even higher than those found in other materials of plant origin. Pollens from gymnosperms, such as pine trees, frequently exhibit low vitamin activities (Sekine and Li, 1950).

Nucleic acids

The nucleic acid content of a few pollens was determined by Sosa-Bourdouil (1949) who found it to be relatively small.

Pollen wall constituents

After the removal of fats, proteins and water soluble material from pollens there is still a relatively high amount of unextractable substance making up between 20 and 57% of the undetermined matter remaining (Todd and Bretherick, 1942). This undetermined material appears to constitute a considerable part of the wall of the pollen grain and is composed of an extremely resistant substance which is commonly found associated with fossil material. The largest component of this mambrane material is pollenin. Zetzsche and Vicari (1931) found it an exceedingly difficult material to characterise. Recently Shaw and Yeadon (1964, 1966) re-examined pollenin and succeeded in breaking it down with ozone and dilute sodium hydroxide into a mixture of simple dicarboxylic acids, lignin and cellulose.

II.5 Larval honeybee nutrition

Introduction

Larval honeybees are fed a special food supplying all the necessary materials for complete development of all three honeybee castes (Johansson and Johansson 1958). This "brood food" is secreted from a pair of pharyngeal glands situated in the head of nurse worker bees, and is a complex mixture of substances (Townsend and Shuel, 1962). Larvae destined to become worker bees have pollen added to their diet when they are over three days old (Jung-Hoffmann, 1966), but this pollen does not supply more than 10% of the nitrogen

required by the larvae (Simpson, 1955). Honey is also added to 'brood food' as a diluent and this mixture is fed to the older larvae facilitating the development of workers rather than queens (Shuel and Dixon, 1959). 'Brood food' is rich in protein (Johansson, 1955), 30 to 35% of the dry matter; this is presumably in part synthesised from the essential amino acids derived from pollen in the adult honeybee diet, because bees cannot rear brood successfully for any length of time unless fresh pollen is supplied to them (Haydak, 1963). The nutritive value of old pollen can be restored by adding the essential amino acids (Dietz and Haydak, 1965). 'Royal jelly' which is the 'brood food' found in cells when queen honeybees are being reared contains as a major constituent an unusual fatty acid 10-hydroxy-$\triangle^2$-decenoic acid (Barker et al., 1959) which is active against certain micro-organisms (Blum et al., 1959).

Requirements for nutrients

Carbohydrates are the main sources of energy for honeybee larvae but some are apparently of greater value than others (Bertholf, 1927). Little is known about the lipid requirements of larval honeybees (Haydak, 1970) but some lipids seem to be essential for pupation (Petit, 1963). The importance of vitamins for honeybee larvae is poorly understood but pyrodoxine (Haydak and Dietz, 1967) and inositol (Nation and Robinson, 1968) appear to be necessary. Water is indispensable for larval honeybees (Petit, 1963). Very little is known of the mineral requirements of honeybee

larvae (Haydak, 1970). The addition of pollen ash to an artificial diet apparently helped colonies to rear more brood (Nation and Robinson, 1968) and cobalt has been stated to be involved in honeybee growth (Burtov, 1958).

II.6 Adult honeybee nutrition

Introduction

As with many other insects there are differences between adult and larval nutrition. The food of the adult worker honeybee consists of pollen and nectar or honey, and the nutritive value of pollen from different plants varies considerably (Maurizio, 1954; Standifer, 1967). Mixed pollens as foraged by honeybees have a high nutritive value (Vivino and Palmer, 1944) and supply all the necessary materials for the proper development of young mammals (Lunden, 1954).

Requirements for nutrients

Pollen supplies most of the protein to honeybees. After eclosion adult honeybees eat some pollen (Hagedorn and Moeller, 1967) and the nitrogen content of the head, thorax and abdomen increases significantly (Haydak, 1959) due to the development of the pharyngeal glands, flight muscles and fat body respectively (Maurizio, 1954). The amount of pollen necessary for this growth is dependent upon the amino acid composition of the proteins in the pollens and the demands by the honeybees for essential acids supplied

by the pollens. Ten amino acids are essential for the growth of adult honeybees, arginine, histidine, lysine, tryptophan, phenylalanine, methionine, threonine, leucine, isoleucine and valine (Groot, 1953); the same ten which are essential for normal growth in rats. Serine, glycine and proline, although not essential cannot be synthesised by the honeybee at a rate that produces optimum growth.

Water plays an important role in the life of honeybees. It is used in large amounts by colonies during the active season to dilute honey and to help regulate the temperature in the brood nest (Lindauer, 1955). Lindauer claimed that honeybees obtain water from their metabolic processes as well as from nectar and from small pools.

Nectar and honey, which are mainly mono and disaccharides, are used as food by honeybees (White, 1957). Their carbohydrate requirements have been determined by feeding various sugar solutions to groups of honeybees and comparing their longevity with others receiving pure water (Vogel, 1931). Honeybees can utilise dextrins and pollen starches but, as intact starch grains from other sources are protected by a coat of amylopectin, these remain unaffected by honeybee diastase (Lotmar, 1935). Carbohydrates normally supply the energy used by honeybees for flight (Beutler, 1936).

The requirements of adult honeybees for lipids, vitamins and minerals have not been studied to any great extent (Haydak, 1970).

II.7 The composition of honeybees

Perhaps the earliest comprehensive analysis of honeybees was that of Straus (1911), who produced information on the dry matter, lipid and crude protein content at various stages of the life cycle. The only fairly detailed mineral analysis was performed on the drone caste and may have included their intestinal contents (Aronssohn, 1911). No further analytical work was published until Haydak (1933) investigated the water and nitrogen content of adult workers of various ages, but did not include the abdomen in this study. Similar analyses concerned with utilisation of pollen protein were performed by Keller-Kitzinger (1935) and Lotmar (1939). Mellampy et al (1939; 1940) determined the water, nitrogen, ash and calorific values of larval and pupal workers and queens. Changes in the weight and nitrogen content of worker honeybees of different ages were reported by Groot (1953). Haydak (1959) repeated his earlier study on the water and nitrogen content of honeybees and extended it to include the abdomen. Hocking and Matsumura (1960) analysed the water, ash, protein, fat and glycogen content of mature larvae and pupae.

II.8 Honey chemistry

The nectar produced by flowers contains on average between 60 and 80% water the remainder is mostly sucrose (Park, 1922). On processing this nectar into honey the honeybees reduce the water content to between 17 and 18% and invert most of the sucrose into glucose and fructose. Honey is hygroscopic, fairly viscose and has, in a good sample, a specific gravity of about 1.41. The water content is one of the most important factors about a honey influencing its keeping quality, granulation and viscosity. Honey is primarily a carbohydrate material with 95 to 99.9% of its solids being sugars (see Table II.1), it is also acidic due to the presence of citric, malic, succinic and other organic acids the most important of which is gluconic acid derived from glucose (Stinson et al., 1960). Traces of amino acids have also been found (Komamine, 1960). The ash content of honey averages about 0.17% of its weight but varies widely. Schuette and his associates (1932, 1937, 1938 and 1939) examined the composition of honey minerals in about one dozen light and dark honeys and some of the more important values are given in Table II.2. Generally, light honeys are poorer in minerals than dark honeys. Enzymes are also found in honey. The most important is invertase which converts the sucrose of nectar into glucose and fructose. Diastase is also found. Honey contains small amounts of vitamins. Haydak et al. (1942) found thiamin, riboflavin, ascorbic acid, pyrodoxine, pantothenic

acid and nicotinic acid in low and very variable amounts. Honey dextrins unlike starch dextrins are long chains of fructose-containing sugars (Fellenberg and Ruffy, 1933). Colloids are present in honey in small amounts especially in dark honeys. The aroma and flavour of honeys which are the most important characters for the consumer have not had much work done on them.

TABLE II.1

Composition of extracted honey (White, 1963)

Components	%
Water	17.20
Fructose	38.19
Glucose	31.28
Sucrose	1.31
Maltose and other reducing disaccharides	7.31
Higher sugars	1.50
Acids	0.57
Proteins (N x 6.25)	0.26
Ash	0.17
Minor components (pigments, vitamins, enzymes etc)	2.21
Totals	100.00

TABLE II.2

Some mineral constituents of honey (as parts per million of total honey composition)

Element	Honeys	
	Light	Dark
Potassium	205	1676
Calcium	49	51
Sodium	18	76
Phosphorus	35	47
Magnesium	19	35
Manganese	0.30	4.09

III OBJECTS OF STUDY

This study was intended to examine certain aspects of honeybee nutrition in the South-East of Scotland with particular reference to pollen, the ultimate source of most if not all of the protein and essential amino acids for honeybees. It was decided to establish the pattern of pollen intake throughout the year, the pollen types utilised by honeybees and the proportions of each collected. This study would also include a chemical analysis of some of the more important pollens in order to ascertain the extent to which these pollens would be able to satisfy the apparent nutritional requirements of honeybees. In addition the pattern of nectar intake, which is the main source of carbohydrate for honeybees, would also be studied and the effects of different nectar flows upon colonies examined. Comparisons between pollen and nectar as sources of minerals for honeybees would also be carried out.

The main experiments performed to achieve these objects are detailed in part IV.

IV EXPERIMENTAL MATERIALS AND METHODS

IV.1 Introduction

The relationship between the honeybee and the available food supply in the South-East of Scotland was studied in several different ways.

1. A 3 years study (1963-1965) of the pollens harvested by 2 colonies of honeybees at Bush Estate when nearly 200 samples of pollen were collected and identified.
2. A 3 years study (1964-1966) of nectar flows in the South-East of Scotland using honeybee colonies on weighing machines in the Lothians' coastal area and in the upland area lying inland from that coast (180 colony weighings).
3. An examination of the effects of environment and pollen traps on colonies of honeybees in 1969 on 4 sites (2 coastal and 2 upland) in the South-East of Scotland to confirm and extend the findings of the 2 studies above. Throughout the season observations were made on 24 colonies and their contents of adult bees, brood, honey and pollen were noted (672 observations). Pollen traps were also fitted to 16 of these colonies and over 250 samples of pollen gathered for identification.
4. Chemical analyses of pollens, honeys and honeybees were also carried out to provide a basis for characterising the nutritional value of the various main pollens gathered and particularly of their amino acids.

IV.2 Pollen harvesting 1963-1965

Pollen traps: The pollen traps used in this investigation (Figure IV.1) were similar to those employed at Rothamsted by Free and Spencer-Booth (1961) and which Free (1967) claimed removed about 10% of the pollen loads from the returning foragers. The efficiency of the trap had been tested by counting the number of pollen gatherers entering it and then counting the pollen pellets lying on the floor of the trap tray (Free, pers. comm.).

Colonies of honeybees: The colonies were selected from a strain bred at Bush for many years. At the beginning of the season colonies were chosen that were apparently equal in strength; they were checked for disease at the beginning and end of each season. Manipulations of the colonies were limited to swarm prevention measures, and only colonies containing queens reared in the previous year were used. Different colonies were selected each year for pollen trapping because it could not be guaranteed that they would survive into the following season. In an attempt to reduce the possible effects of congestion at the hive entrance caused by the pollen traps, slightly smaller colonies (covering only about 6 standard frames in late spring) were selected in the seasons 1963 to 1965. Smith beehives (Anon, 1960) were used to house the colonies; additional chambers were added as required.

Experimental: In a preliminary investigation pollen traps were fitted to colonies of honeybees in January and the

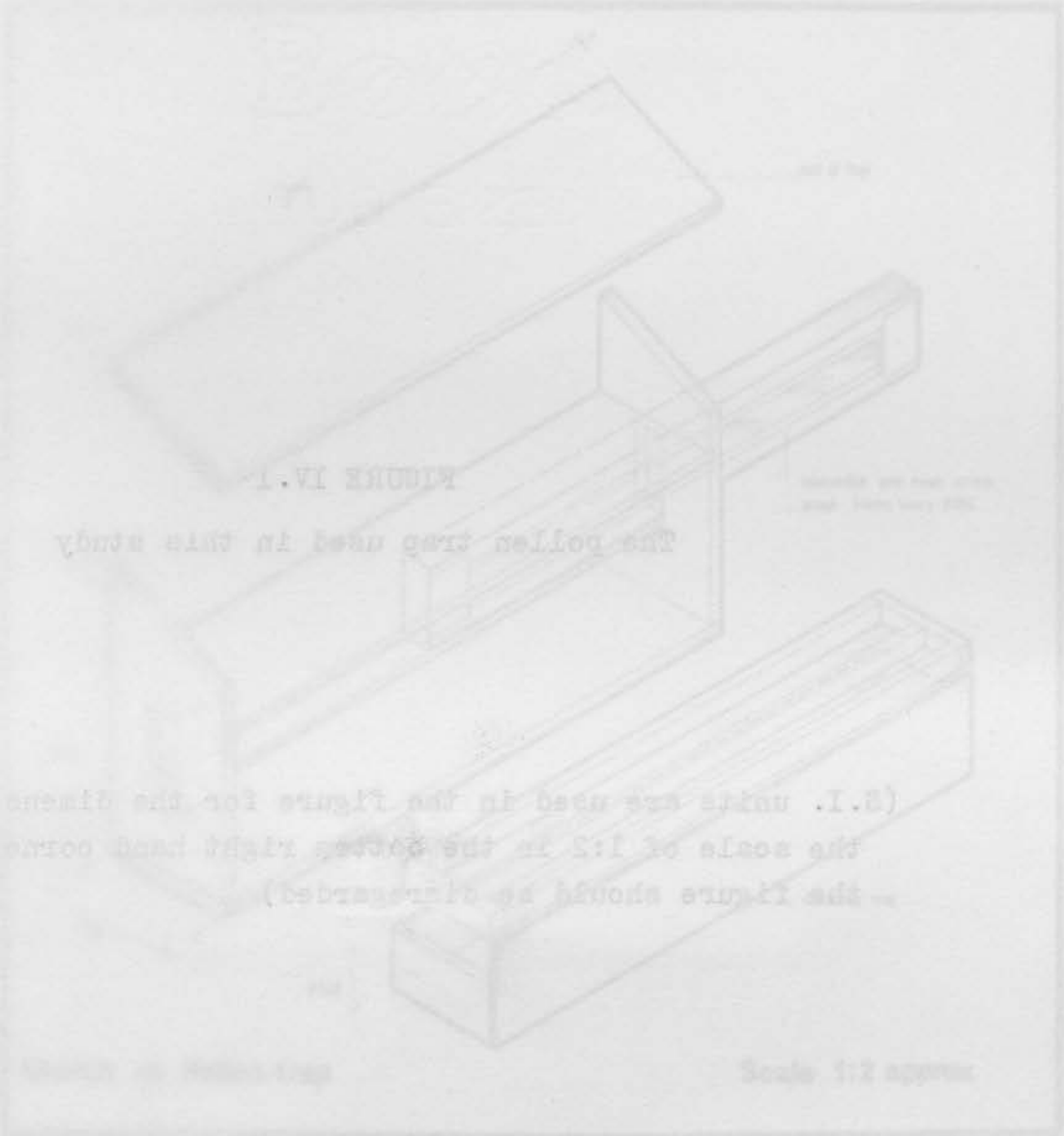
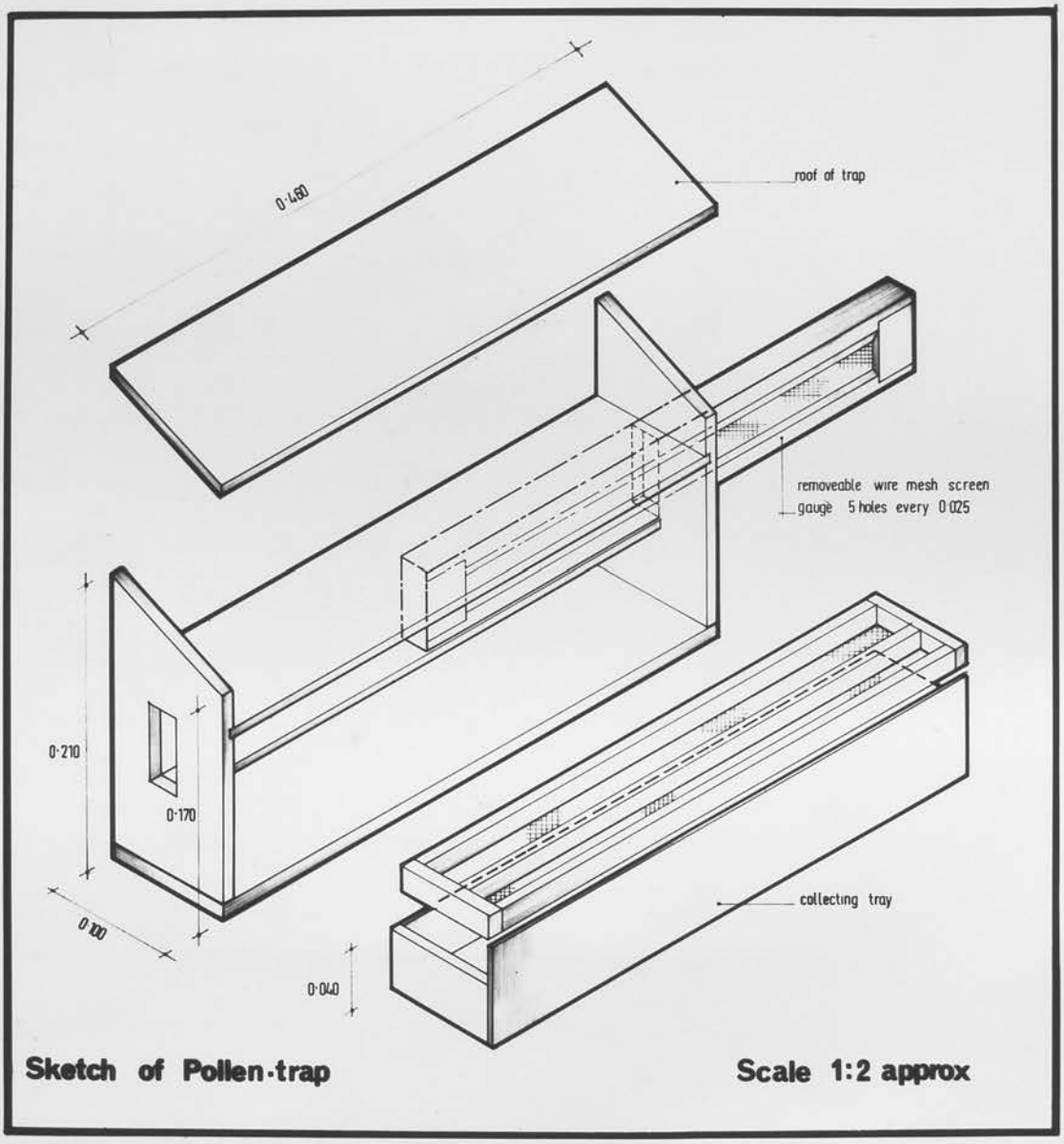


FIGURE IV.1

The pollen trap used in this study

(S.I. units are used in the figure for the dimensions; the scale of 1:2 in the bottom right hand corner of the figure should be disregarded)



Sketch of Pollen-trap **Scale 1:2 approx**

harvest of pollen at Bush site (Figure IV.3)throughout the year was noted. It was thus established that pollen was gathered in quantity only between mid-May and late September. Thereafter traps were fitted to colonies at the beginning of May and removed at the end of October (September in 1969). The pollen collected was placed in paper bags and stored at -20°C until examined. The site at Bush is described in Section IV.4.

IV.3 Pollen sampling and identification

In this investigation sub-samples of 4 g of pellets were removed from each pollen harvest[1](Plate IV.1) for identification. This provided a reasonable degree of accuracy for all pollens except those present in small quantities. (Appendix 11).

The sample of pollen pellets was weighed and placed on a sheet of black glass. The individual pellets were then separated on the basis of colour and texture into groups which were weighed (Louveaux, 1958). Bright sunlight was the best aid to this operation but if this was unobtainable a strong electric lamp was used instead. Although mixed loads were occasionally found they were excluded from the pellets used in the identification.

Each group of pellets was placed in a mortar, a few drops of distilled water added and the whole ground up into a fine paste. Samples of the mixture were then placed on clean microscopic slides, stained and examined.

[1]That is each pollen collection removed from a pollen trap.

PLATE IV.1

Pollen pellets from a pollen trap

Two methods of making microscope slides of pollen grains were used. The first was described by Maurizio (1951). While the other, Method 2, was gradually evolved during the course of this investigation.

Method 2.

1. Grind up the pollen pellets in a little water.
2. Place a drop of this mixture on a microscope slide.
3. Spread out the grains until they are fairly well separated.
4. Dry with a hot air hair-drier.
5. Add a few drops of 70% ethyl alcohol, to expand the grains and to clean the oil from them.
6. Add a drop of basic fuchsin, and dry with a hair-drier.
7. Add a drop of euparal vert (mounting medium).
8. Add a cover slip.
9. Heat in an oven until the euparal sets hard.
10. Label and store.

Three microscope slides of each pollen type were prepared for reference purposes.

The pollen slides were examined under the low, high and oil immersion lenses of a compound microscope for identification. After an introductory period, the more common pollens could be identified fairly easily by their shape and surface texture. The keys, diagrams and photomicrographs of Armbruster and Oenike (1929), Zander (1935),

Hodges (1952), Faegri and Iversen (1953), and Maurizio and Louveaux (1965) were all used, as was also a collection of type pollens prepared directly from important pollen plants.

By these methods most of the pollens were identified and separated into either families or species. The generic and specific epithets used were those of the second edition (1962) of the 'Flora of the British Isles' by Clapham, Tutin and Warburg. For simplicity the common English names are used often in the text; the equivalent Latin binomials are all given in Appendix 1 where the floral composition of the sites is described.

It was extremely difficult to identify certain pollens and so it was felt that it would be more satisfactory to classify them into genera or families; this was particularly the case for the Cruciferae. Where difficulties in identifying pollens were experienced, pollen experts were consulted and eventually all but a very small fraction of the pollens gathered were classified.

The results of pollen trapping were expressed in tabular form in Appendices 3 and 4. The weights of each pollen type in grams and the percentage of the total amount gathered were calculated and included in these tables.

Where the term pollen type is used it refers to the species, genus or family into which that particular pollen was classified.

IV.4 The effects of environment and pollen traps on colonies of honeybees

Introduction

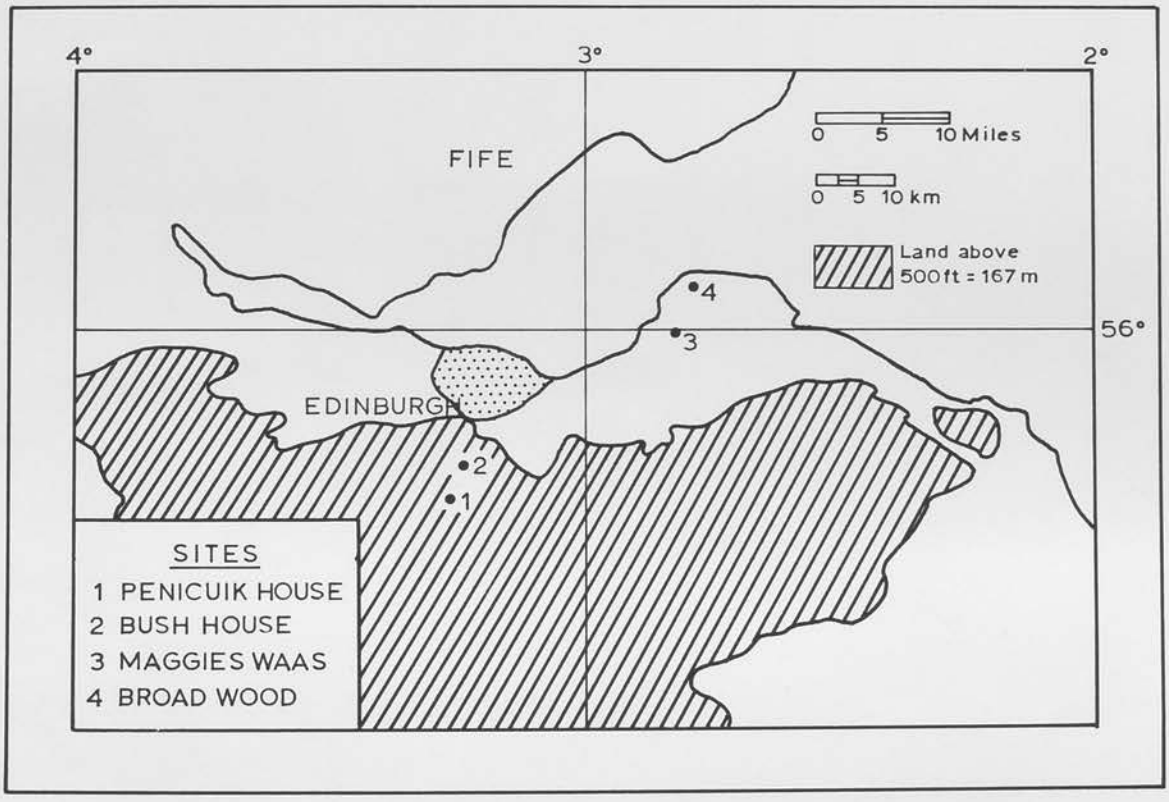
In 1969 the pollen harvesting and nectar flow analyses were extended to the 2 areas where the nectar flow patterns had already been established so that the general effects of different environments and pollen traps on colonies of honeybees could be examined. The effects were estimated by inspecting 24 colonies on 4 sites, 2 inland, at Penicuik and Bush, and 2 coastal, at Broadwood and Maggie's Waas (Figure IV.2) during the active season from May to the end of September in 1969 and measuring the numbers of adult honeybees and brood and the amounts of honey and pollen stored and trapped. The adult honeybees were determined by a visual method of comparison with standard photographs of known numbers of honeybees on combs (Jeffree, 1951). Inspections were conducted, as far as possible, when few foragers would be out of the hives. This had been found satisfactory and was preferable to shaking the bees from the combs and weighing them because any nectar shaken from the combs would have increased the weight of the bees (Allen and Jeffree, 1956). The total brood (which included eggs, larvae and pupae), pollen and honey stored, were then measured by a graduated grid after honeybees had been shaken from the combs (Jeffree, 1958a).

Sites

On the coastal sites of East Lothian, the main nectar flows occurred early in the season but on the inland sites

FIGURE IV.2

Pollen collecting sites 1969

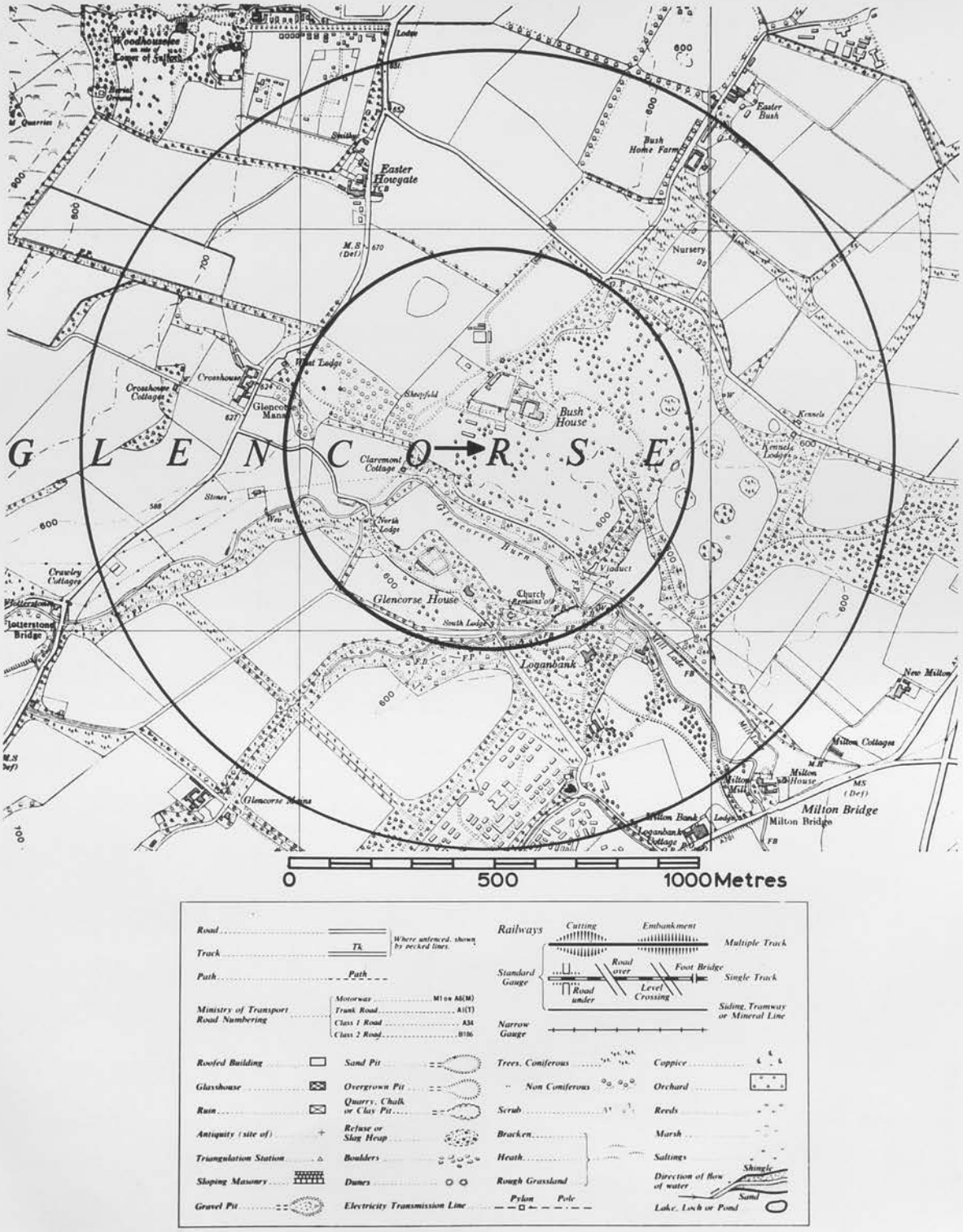

4°
3°
2°
56°
FIFE
EDINBURGH
0 5 10 Miles
0 5 10 km
Land above
500ft = 167m
SITES
1 PENICUIK HOUSE
2 BUSH HOUSE
3 MAGGIES WAAS
4 BROAD WOOD

in Midlothian there were, in addition, late summer nectar flows. All sites were situated at least 5 km from each other. As honeybees do not forage much beyond 400 to 500 metres under normal circumstances (Beutler, 1954; Sedivy et al, 1966) it was considered unlikely that honeybees from these different sites would be utilising the same flowers (Ribbands, 1953). The general land use (Table V.25) and the relative abundance of pollen producing plants within 1000 metres of each site that might be utilised by honeybees were noted (Appendix 1).

Bush House site: This site (Figure IV.3) was situated on the Bush Estate, Milton Bridge by Penicuik, Midlothian, grid reference NT 246 636, altitude 184 metres. The area sloped gradually upwards from just under 180 m in the south-east to over 210 on the north-west and was traversed from west to south-east by the Glencorse Burn which flows in a shallow valley. The soil pH lay between 5 and 7 and although the soil types are very mixed they are predominantly imperfectly drained sandy clay loams mainly of the Macmerry series (Scottish Soil Survey). As the 'Haggs', the former name of Bush House suggests this area was mainly covered with peat but this was removed and large covered drains were constructed in the agricultural improvements of the late 18th century. A large part of this area was planted with trees at this period in an attempt to enliven the landscape and make it appear less bare than it had formerly been; more recently conifers have been planted where

FIGURE IV.3

Bush House site



Road
Track — Tk
Path — Path
Where unfenced, shown by pecked lines.

Ministry of Transport Road Numbering
Motorway — M1 or A6(M)
Trunk Road — A1(T)
Class 1 Road — A34
Class 2 Road — B186

Roofed Building
Glasshouse
Ruin
Antiquity (site of) +
Triangulation Station △
Sloping Masonry
Gravel Pit
Sand Pit
Overgrown Pit
Quarry, Chalk or Clay Pit
Refuse or Slag Heap
Boulders
Dunes
Electricity Transmission Line

Railways
Cutting
Embankment
Multiple Track
Standard Gauge
Road over
Foot Bridge
Single Track
Road under
Level Crossing
Siding, Tramway or Mineral Line
Narrow Gauge

Trees, Coniferous
Non Coniferous
Scrub
Bracken
Heath
Rough Grassland
Pylon
Pole
Coppice
Orchard
Reeds
Marsh
Saltings
Direction of flow of water
Shingle
Sand
Lake, Loch or Pond

deciduous trees have been cut down.

The largest part of the area is covered with either amenity grassland or pasture, and arable crops occupy the next largest area. Woods are also a prominent feature, along the Glencorse Burn and its tributaries, around the country houses and further afield as shelter belts. A few new buildings have been erected on the Bush Estate and on the Ministry of Defence property surrounding Glencorse Barracks in the south of the area in the past few years. The grassland within the area is of several types; pasture land which has usually been reseeded by a short term ley of grass and white clover (Trifolium repens), parkland areas which, in addition to grasses, contain white clover (Trifolium repens), daisy (Bellis perennis), yarrow (Achillea millifolium) and self heal (Prunella vulgaris) and road and field verges, with silverweed (Potentilla anserina) and species resistant to mineral oils (Umbelliferae) common especially on road verges. The open mixed woodland areas contain an abundance of rosebay willow-herb (Chamaenerion angustifolium), rhododendron (Rhododendron ponticum) and raspberry (Rubus idaeus) with large patches of buttercups (Ranunculus spp.) in the shaded grass. Cruciferous weeds (Raphanus raphanistrum and Sinapis arvensis) and dead nettles (Lamium spp.) were common in the arable fields (Appendix 1).

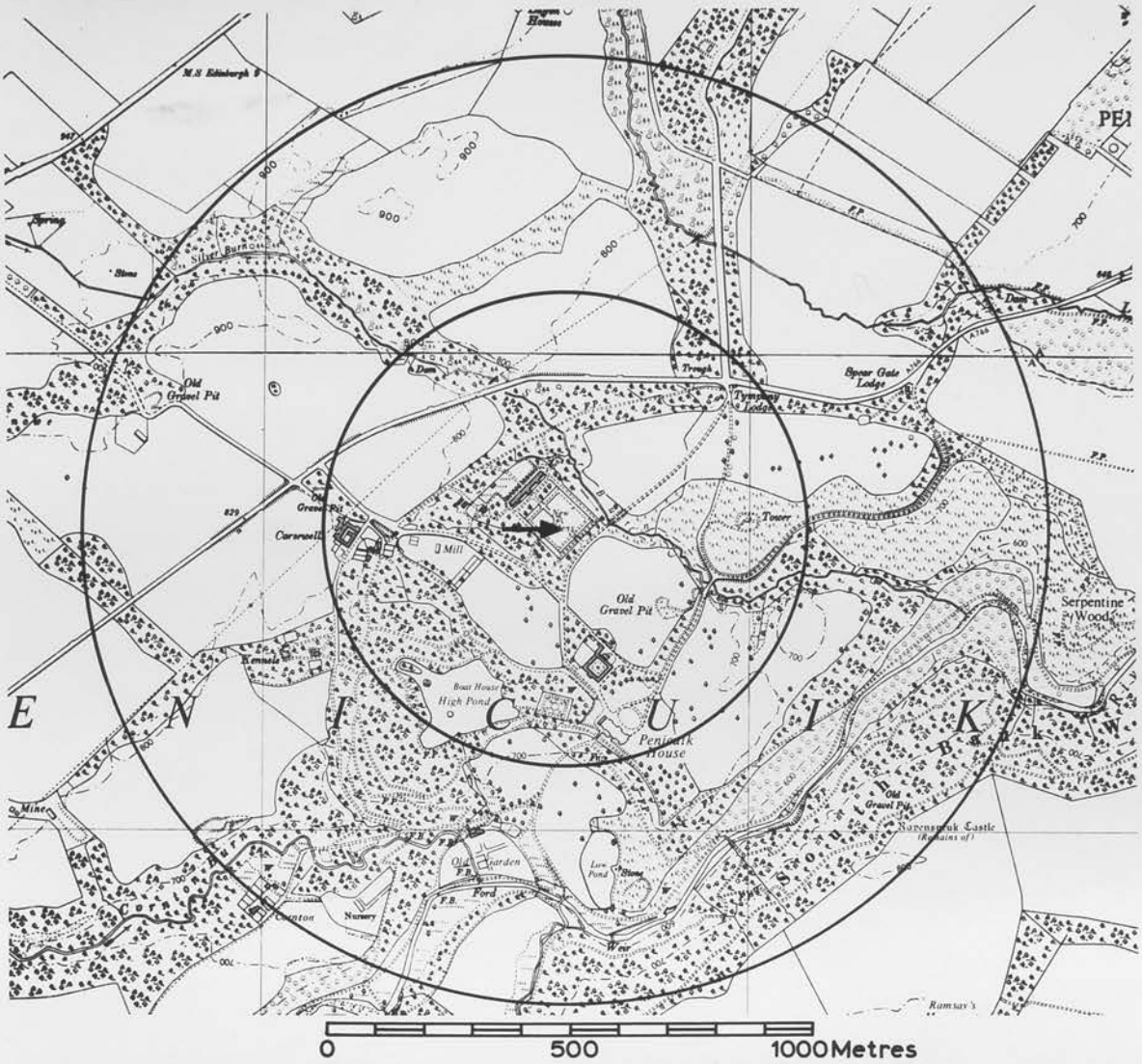
The weather at Bush is summarised in Tables V.35 (1964-1966), 8.1 (temperatures 1963-1965), 8.2 (1969).

August is normally the wettest month during the active season of the honeybee and June the driest.

Penicuik House site: This lies on the Penicuik Estate, Penicuik, Midlothian, grid reference NT 216 596, altitude 225 metres. The area considered (Figure IV.4) which lay within 1000 metres of the site rose from just under 180 metres on the south and east to just over 270 metres on the north-west. On the south and south-east it is traversed by the North Esk River and the ground falls away steeply in places down to the river. There was extensive planting of trees (Acer pseudoplatanus, Quercus spp., Fagus sylvatica, Ulmus spp., Larix decidua and Pices abies) and shrubs, particularly rhododendron, (Rhododendron ponticum) during the late 18th and early 19th centuries when two large ponds lying to the south of the site were developed. Generally the area is covered with trees especially on the steeper parts but in the flatter areas fields used for cropping or pasture were present. Most of the woodlands are mixed, but a large plantation of conifers planted more recently extends from the middle to the east of the site. Flowering wild plants are common in the open woodland areas and by the field and road verges. Rosebay willow-herb (Chamaenerion angustifolium), thistle (Cirsium spp.) meadow sweet (Filipendula ulmaria), raspberry (Rubus idaeus), buttercups (Ranunculus spp.), and birds foot trefoil (Lotus corniculatus) were common and other species are listed in Appendix 1. Within the past decade the town of Penicuik has been

FIGURE IV.4

Penicuik House site



Road
Track — Tk
Path — Path
Where untenced, shown by pecked lines.

Ministry of Transport Road Numbering
Motorway — M1 or A6(M)
Trunk Road — A1(T)
Class 1 Road — A34
Class 2 Road — B186

Railways
Cutting
Embankment
Multiple Track
Standard Gauge
Road over
Foot Bridge
Single Track
Road under
Level Crossing
Siding, Tramway or Mineral Line
Narrow Gauge

Roofed Building
Glasshouse
Ruin
Antiquity (site of)
Triangulation Station
Sloping Masonry
Gravel Pit
Sand Pit
Overgrown Pit
Quarry, Chalk or Clay Pit
Refuse or Slag Heap
Boulders
Dunes
Electricity Transmission Line

Trees, Coniferous
Non Coniferous
Scrub
Bracken
Heath
Rough Grassland
Pylon
Pole

Coppice
Orchard
Reeds
Marsh
Saltings
Direction of flow of water
Shingle
Sand
Lake, Loch or Pond

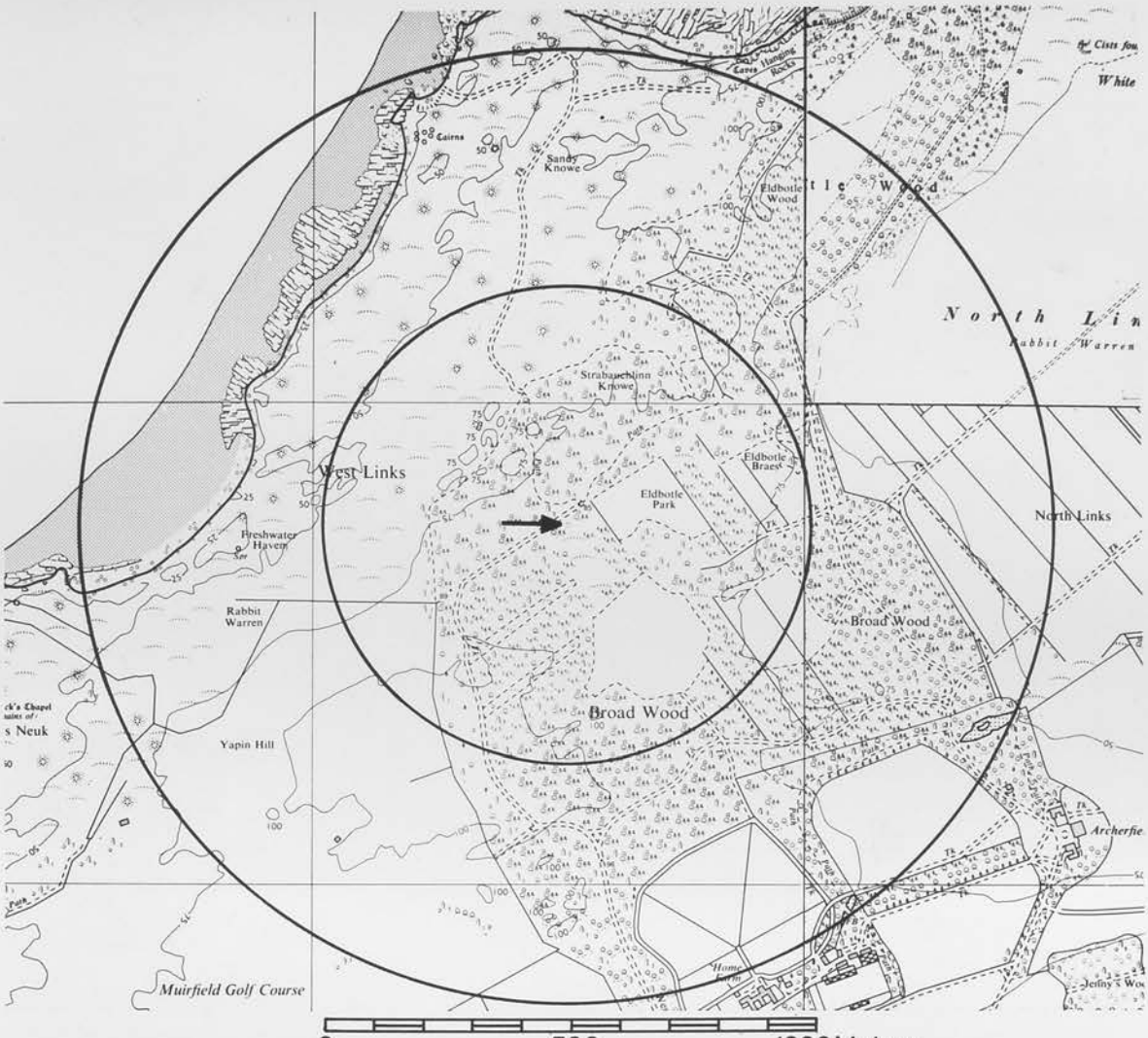
extended to occupy the extreme north-east of this area. The weather at Penicuik during the active season in 1969 is summarised in Table 8.2 of the Appendix. Generally May was colder and wetter than average but June, July, August and September were drier and warmer than average. Although the colonies were sited in the middle of the 'New Gardens' these 'Gardens' were being used to produce 'Christmas trees'. The soil pH within the area varied from about 5 to 7 and was mostly of the Darvel series (Scottish Soil Survey). Generally the flora and climate on Bush and Penicuik sites were very similar.

Broadwood site: This coastal site (Figure IV.5) was on the Archerfield Estate, Dirleton, East Lothian, grid reference NT 495 845, altitude 25 metres. It is a fairly flat area, except on the south-west and north-east where there are 2 parts over 30 metres above mean sea level which are joined by a ridge 25 metres high. The ground also slopes gradually down to the sea on the north-west side. Most of the soil has a pH between 7 and 8 and is mainly composed of freely drained loamy sand to sandy loam predominantly of the Fraserburgh soil series, although some of the land on the extreme east side of the site lying below 17 metres altitude has a tendency to become waterlogged.

The north-west of the site consisted of sand dunes covered with marram (Ammophila arenaria) and lyme grass (Elymus arenarius) with meadow grasses frequent further from the sea. Patches of sea buckthorn (Hoppophae rhamnoides)

FIGURE IV.5

Broadwood site



Road
Track — Tk
Path — Path
Where unfenced, shown by pecked lines.

Ministry of Transport Road Numbering
Motorway — M1 or A6(M)
Trunk Road — A1(T)
Class 1 Road — A34
Class 2 Road — B186

Roofed Building
Glasshouse
Ruin
Antiquity (site of)
Triangulation Station
Sloping Masonry
Gravel Pit
Sand Pit
Overgrown Pit
Quarry, Chalk or Clay Pit
Refuse or Slag Heap
Boulders
Dunes
Electricity Transmission Line

Railways
Cutting
Embankment
Multiple Track
Standard Gauge
Road over
Foot Bridge
Single Track
Road under
Level Crossing
Siding, Tramway or Mineral Line
Narrow Gauge

Trees, Coniferous
Non Coniferous
Scrub
Bracken
Heath
Rough Grassland
Pylon
Pole
Coppice
Orchard
Reeds
Marsh
Saltings
Direction of flow of water
Shingle
Sand
Lake, Loch or Pond

introduced into this area from England in the 18th Century to stabilise the sand and provide shelter belts were to be found frequently on the landward side of the dunes. On the west side of the site there was a golf course which was covered with grass. Grass was also frequent in most of the woodland glades, on wasteland at the edge of the woods, and in pasture on the east of the site. Mixed woodland which ran from the north-east corner to the south-south-east side of the site occupied the second largest part of the area. Freely regenerating sycamore (Acer pseudoplatanus) was very common in the woodland and wild privet (Ligustrum vulgare) and elderberry (Sambucus nigra) were frequent on the woodland edges. Hawthorn (Crataegus monogyna) hedges were common as field boundaries. Towards the middle of the woodlands there was a plantation of coniferous trees of various ages consisting mainly of Scots and Corsican pines (Pinus sylvestris and Pinus nigra laricio). A few fields of grain and potatoes were found within the area otherwise mainly occupied by woodland and also on the east and south of the main area. The flowering herbs were found scattered in the predominantly grassy ground cover particularly in the woodland clearings, the waste land surrounding the woods and the field boundaries and around the tracks leading through the woods. Generally few flowers were conspicuous and only vipers bugloss (Echium vulgare), speedwells, (Veronica chamaedrys and V. officinalis) and forgetmenot (Myosotis arvensis) were locally abundant; one piece of

wasteland between the woods and the golf course was covered with thistles (Carduus and Cirsium spp.) (Appendix 1).

This is one of the driest areas of Scotland, annual rainfall 654 mm (25.69 inches) according to the nearest rainfall station (East Fortune Hospital). In the active period of the honeybee year the wettest month was August and the driest June. May and June in 1969 were wetter than average but the other months were drier.

Maggie's Waas site: This site (Figure IV.6) lies on the Luffness Estate, Aberlady, East Lothian, grid reference NT 478 795, altitude 10 metres. The area was almost uniformly flat and lay between 8 and 17 metres above mean sea level. Most of the land was occupied with arable farming (potatoes, grain, sugar beet and turnips). Maggie's Waas Wood consisted mainly of deciduous trees although there were a few conifers. Two shelter belts of trees ran north from Maggie's Waas Wood to join other shelter belts surrounding Luffness House Park. The trees were mainly Acer pseudoplatanus, Fagus sylvatica, Quercus spp., and even a few Betula spp., on a piece of shrubland on the east of the site with conifers such as Picea abies, Pinus spp. and a few Taxus baccata. In addition to Luffness House, there were two farms and three small holdings lying within the area indicating the intensive land use of most of its surface. The soil whose pH lay between 5 and 6.5 was mainly composed of fine sandy loams and silts

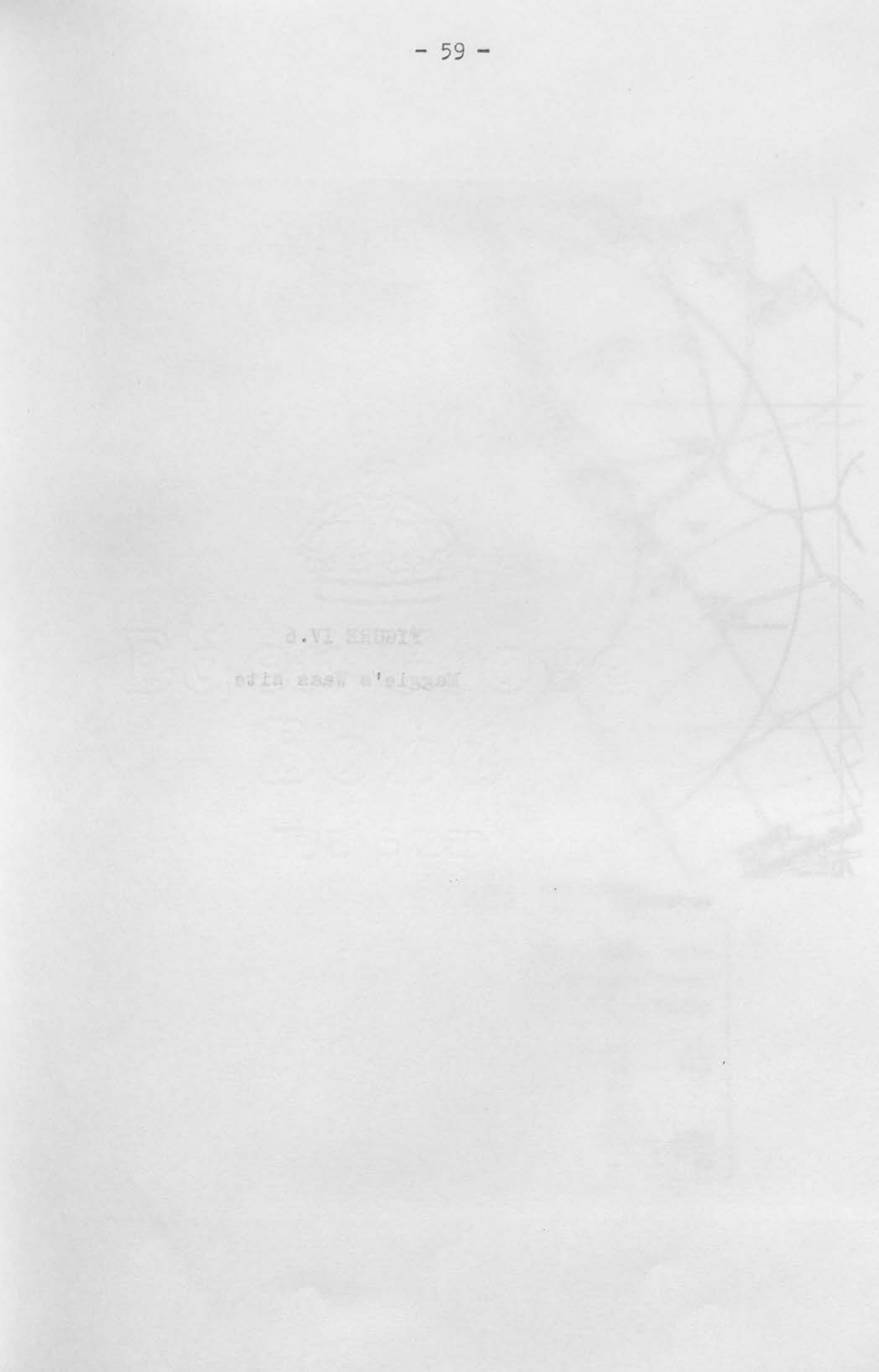
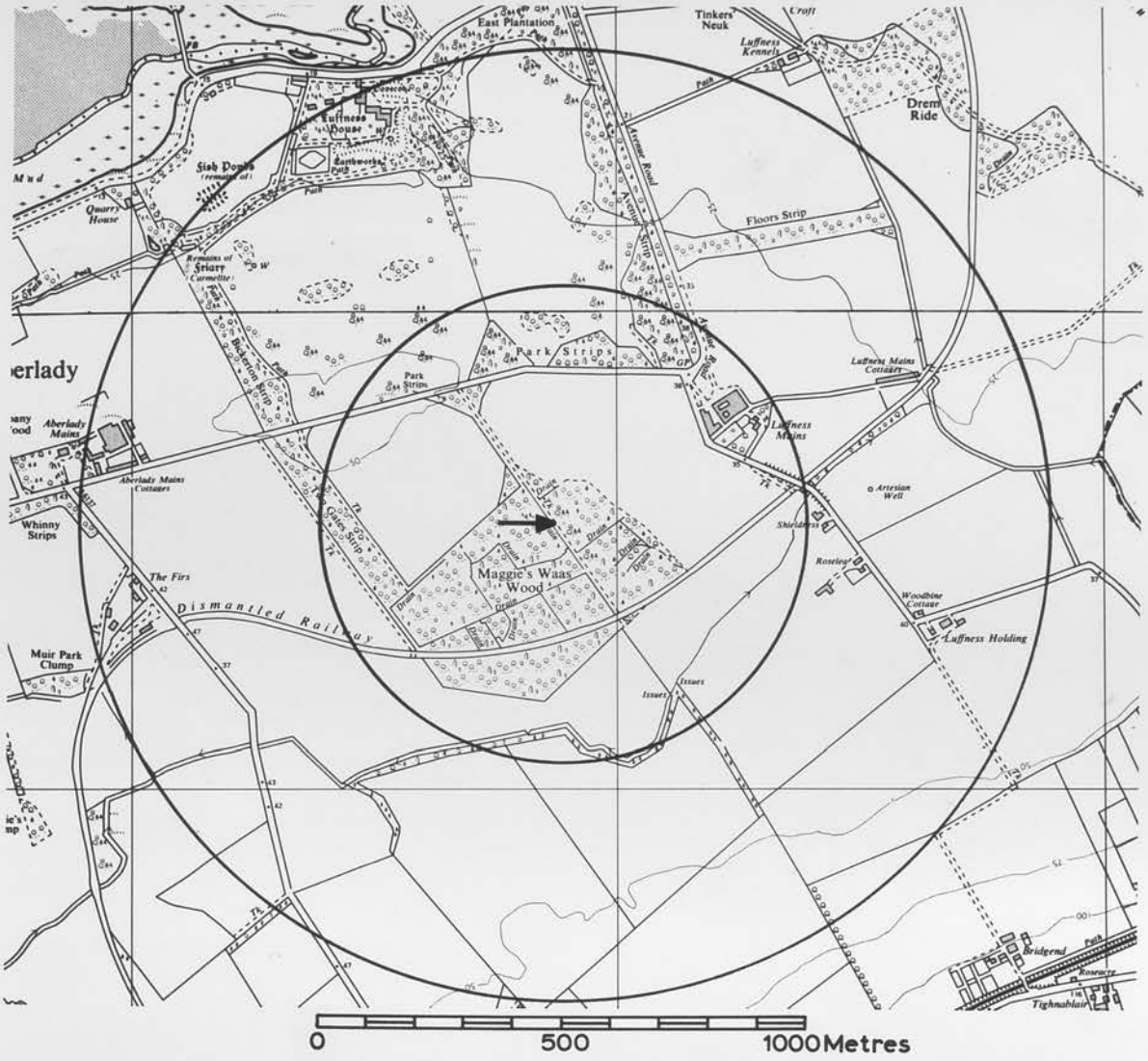


FIGURE IV.6

Maggie's Waas site



Road ..... Where unfenced, shown by pecked lines.
Track ..... Tk
Path ..... Path

Ministry of Transport Road Numbering
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Roofed Building
Glasshouse
Ruin
Antiquity (site of) +
Triangulation Station △
Sloping Masonry
Gravel Pit

Sand Pit
Overgrown Pit
Quarry, Chalk or Clay Pit
Refuse or Slag Heap
Boulders
Dunes
Electricity Transmission Line

Railways
Standard Gauge
Narrow Gauge
Cutting
Embankment
Road over
Road under
Foot Bridge
Level Crossing
Multiple Track
Single Track
Siding, Tramway or Mineral Line

Trees, Coniferous
Non Coniferous
Scrub
Bracken
Heath
Rough Grassland
Pylon
Pole

Coppice
Orchard
Reeds
Marsh
Saltings
Direction of flow of water
Shingle
Sand
Lake, Loch or Pond

of the Dreghorn series. Poor drainage was a feature of the area because of the soil type and the low lying aspect of the land and in an attempt to improve the situation in Maggie's Waas Wood large drains had been dug. There were few flowers in the depths of the wood because of the scarcity of light and the most frequently occurring vegetation found around cultivated fields and in woodland clearings was grass but generally there was very little permanent grassland within 1000 metres of the colonies. Rosebay willowherb (Chamaenerion angustifolium), and umbells (Umbelliferae) were common on the edges of woods, meadow sweet (Filipendula ulmaria) and buttercups (Ranunculus spp.) in the damper areas and charlock (Sinapis arvensis) and dead nettles (Lamium spp.) in the cultivated fields. The general weather situation was probably very similar to that at Broadwood and in 1969 the weather data were derived from the station at Haddington which was the nearest one to the coastal sites with detailed information of temperature, sunshine and rain.

Colonies

The colonies of honeybees from the college apiary were inspected on 15th May and divided into groups of four. Each site was supplied with a group of 4 colonies to which pollen traps (Synge, 1947) were fitted on 22nd May. (There was a very late spring in 1969 and no pollen was gathered in quantity before this date.) In addition one coastal site (Broadwood) and one inland site (Bush) were supplied with a group of 4 colonies without traps to act as controls.

Each group of 4 colonies was arranged in a circle to minimize the numbers of honeybees drifting into end colonies (Jay, 1966). Pollen collection from the traps began on 25th May and was continued until late September when no more pollen was being harvested by the colonies. In 1969 when it was thought (from the observations of traps operating in 1963, 1964 and 1965) that colonies could apparently cope with the congestion that traps induced at the hive entrance, larger colonies covering at least 8 standard honeycombs with bees in mid-May were used for the experiment. Additional chambers were added to the double brood chambered Smith hives housing the colonies when required. The colonies were also overwintered in double brood chambers.

IV.5 Nectar flows

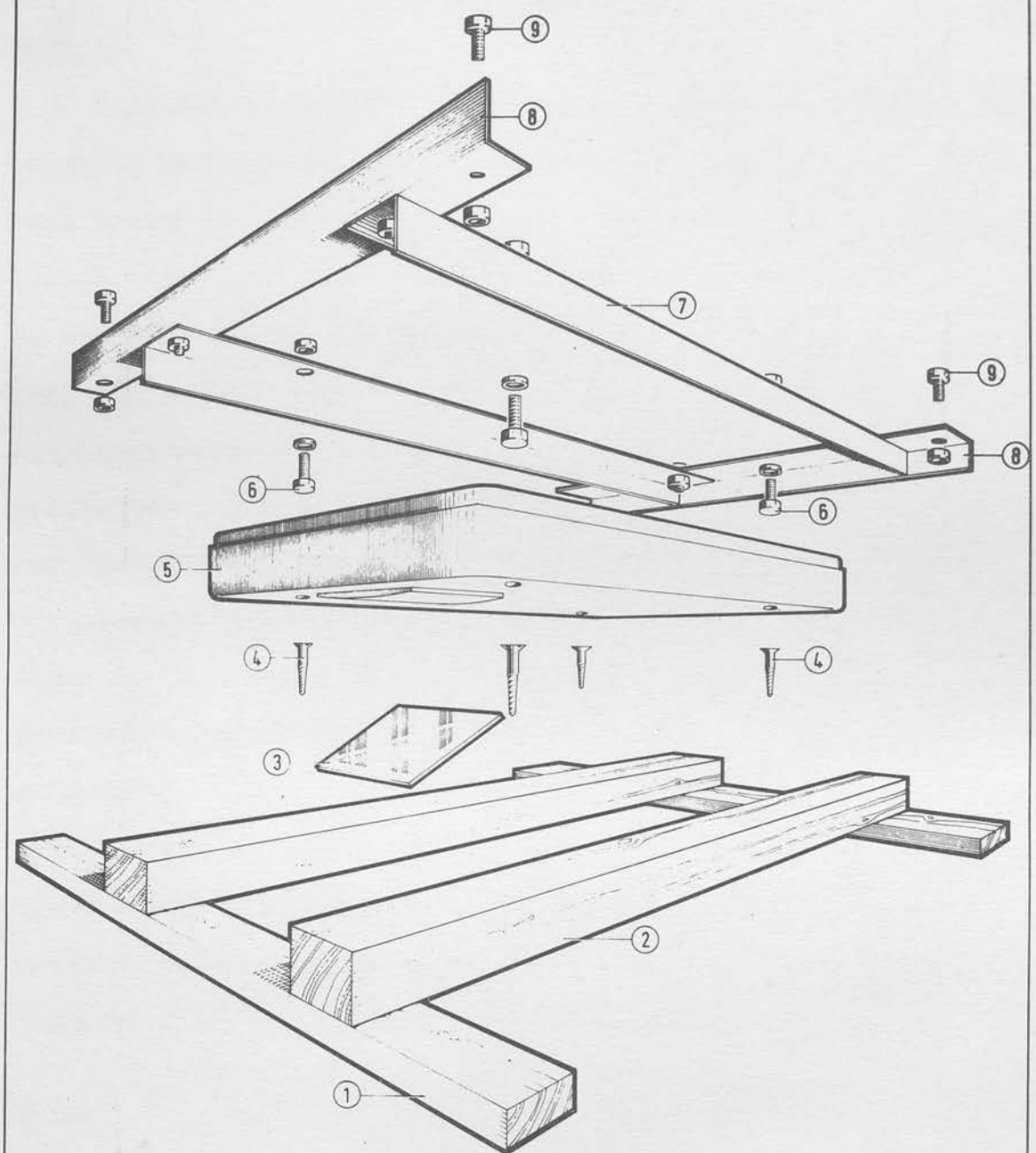
Weighing machines

Several 'Salter 200' personal weighing machines were modified for weighing Smith pattern beehives (see Figure IV.7) because of the expense of commercially-available broad platform weighing machines. Before modification the machines were dismantled and coated with grease and an anticorrosive agent (WD 40) to protect them from the weather. An angle iron framework was constructed to support the base of the hive and screwed to the underside of the weighing machine while wooden supports were attached to the upper surface in order to provide greater stability (see Figure IV.7). These machines were put into operation by inverting them on level ground and placing a beehive upon the angle iron framework. Readings of hive weights were obtained by placing a mirror below the machine as indicated in Figure V.7.

FIGURE IV.7

The hive weighing machine

HIVE WEIGHING MACHINE



1. 2"x1" TIMBER
2. 2"x 2" TIMBER
   — FORMING THE BOTTOM FRAME
3. MIRROR
4. FOUR WOOD SCREWS — SET THROUGH HOLES DRILLED IN THE SCALES TOP
5. BATHROOM SCALES — MOUNTED FACE DOWN
6. FOUR BOLTS WASHERS AND NUTS — SET THROUGH HOLES IN THE SCALES BASE
7. 1½" x 2½" x ⅛" ANGLE
8. 1½" x 1½" x ⅛" ANGLE
   — FORMING THE TOP FRAME
9. FOUR BOLTS AND NUTS — ONE AT EACH CORNER OF THE TOP FRAME TO AID BALANCING OF HIVE

The scale was zeroed by using the knurled adjustment nut. These weighing machines were sensitive to weight changes of 0.5 kg.

Methods

Colonies of honeybees in Smith beehives were placed on weighing machines at selected sites (see Figure IV.8). Each season between 1964 and 1966 inclusive, colonies with queens under one year old were chosen for this experiment in order to reduce the swarming tendency. These colonies were subject to uniform management practices. Regular weighings were performed throughout the season from May to September. The colonies were also weighed before and after any internal inspections. When the weight change of these colonies was calculated, allowances were made for alterations in the weight of the wooden parts of the beehive and drawn comb, as for example when honey chambers were added or removed. The actual weights recorded were those of the total weight of honey, brood, bees, pollen and wax, though there was little alteration of the amount of wax because all colonies were supplied with drawn-comb, so wax secretion was required only for finishing off and capping the cells.

Sites

Three sites on the Lothian coastal area, (Dirleton, Grid reference NT 519 843; Fettes, NT 235 753; Longniddry, NT 443 772) and three in the upland area (Bush, NT 245 635; Houndleshope, NT 235 358; Lauder, NT 520 474) of the South-East of Scotland were chosen because previous observations

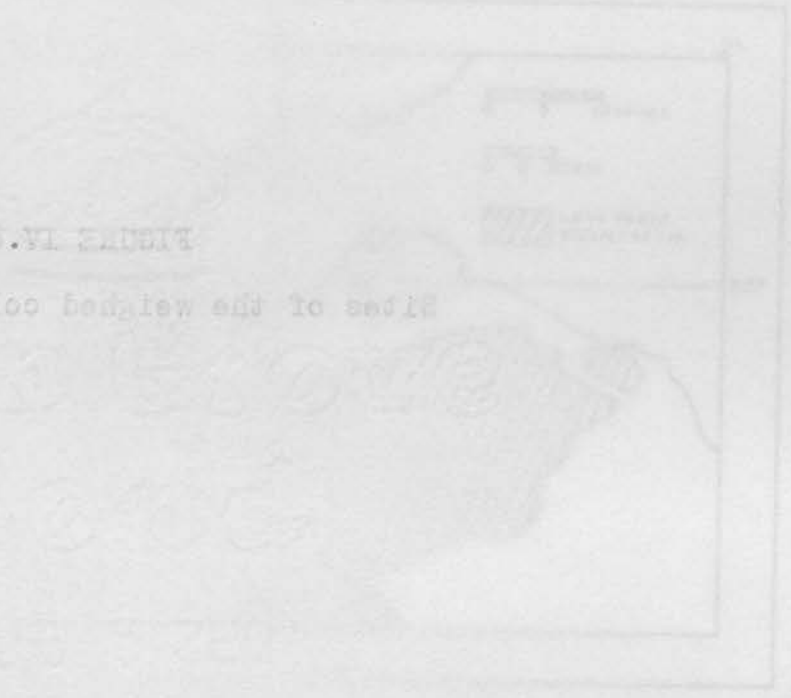
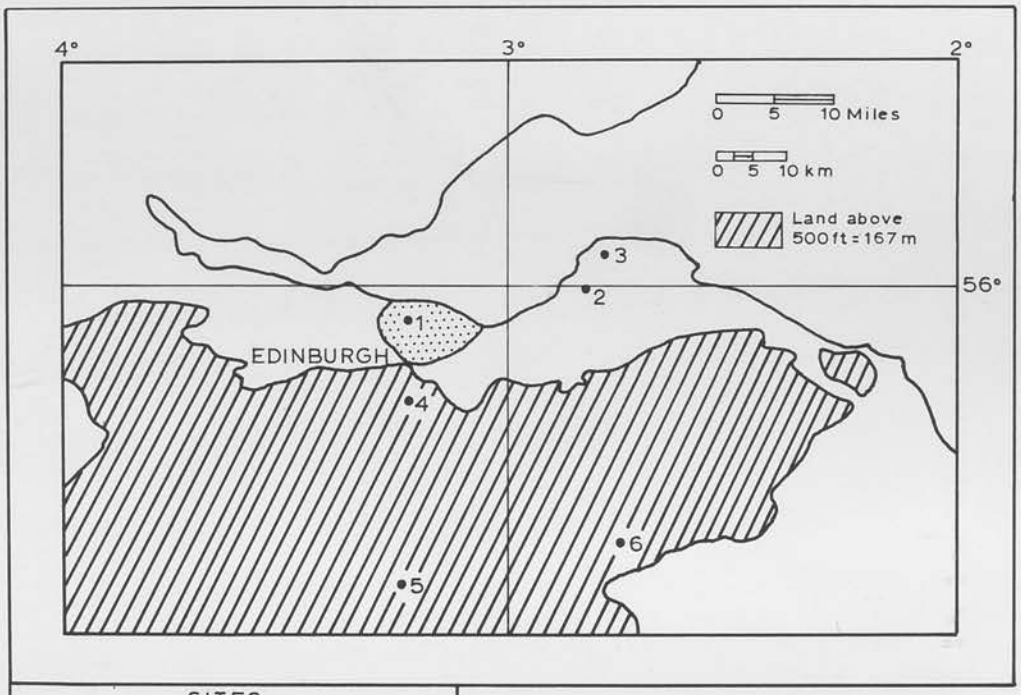


FIGURE IV.8

Sites of the weighed colonies, 1964-1966



SITES

1 FETTES	4 BUSH
2 LONGNIDDRY	5 HOUNDLESHOPE
3 DIRLETON	6 LAUDER

had indicated that the patterns of nectar production from these 2 areas were dissimilar.

The coastal sites were quite separate from each other, the distances between them being much greater than the normal foraging distance of honeybees. All these sites were between 4 and 30 metres above mean sea level and about 2 km from the sea. The Lothian coastal area is one of the driest parts of Scotland and is relatively free from frosts.

The other sites were situated in the upland arable areas more than 12 km south of the coast. They were all over 180 metres (600 feet) above mean sea level and about 1 km from ling heath (Calluna vulgaris) moorland. The climate in these higher areas was generally colder, wetter and windier than on the coast and there was normally a much greater incidence of frost damage each season, particularly to sycamore blossom.

The relationship between honey stored and total colony weight

This was examined throughout the active season in 1969 by determining the correlation coefficients between the weight of honey and total net colony weight (honeybees, honey, brood, pollen and wax) on 7 occasions between May and late September for 24 colonies of honeybees (Appendix 6).

IV.6 Weather

The temperatures at Bush between 1963 and 1965 (Table 8.1) and the weather in terms of the daily means of shade air temperature, sunshine and rain for the active season of 1969 at the weather stations nearest to the sites are described in the Appendix (Appendix 8.2). In addition a general survey of the weather at Bush between 1964 and 1966 (Table V.35) has been included in the results.

IV.7 Units of measurement

Normally S.I. units have been used but in circumstances where Imperial units were normally utilised the latter have been retained.

IV.8 Chemical analyses

Pollen

Sampling: All pollen was weighed when collected and then stored at -20°C until required. The separation of sufficient pollen of one type from the mixed collections for chemical analyses was a very time consuming process. Because of the small size of the pollen grains both the macroscopic appearance of the pellets and the microscopic

texture of the pollen grains were used to separate the different types. Occasionally it was necessary to utilise several different pollen collections to obtain sufficient pollen of any one type for analysis. All analyses were performed in duplicate.

Dry matter: Approximately 2g samples of each pollen were obtained, weighed, dried overnight at 105°C, placed in vacuum desiccators, cooled and weighed again and the dry matter obtained by subtraction. Samples taken at the same time were used for ether extraction, and the determination of nitrogen and carbohydrates.

Ether extractions: Approximately 2g samples of each pollen were separated, milled and extracted in a Soxhlet apparatus with petroleum spirit (B.Pt. 40-60°C) for 16 h. The lipid material was extracted, dried and weighed after cooling in a vacuum desiccator. The material present in this extract consisted of lipids, fat soluble pigments and vitamins, plant waxes and resins (Todd and Bretherick, 1942).

Nitrogen: Nitrogen determinations were carried out on small samples of pollen by the micro-Kjeldahl method (Markham, 1942) as modified by Yuen and Pollard (1953), see Appendix 9.

Carbohydrate estimations: All carbohydrate estimations except those for fructose, glucose and starch were based on a scheme for the examination of the carbohydrates of plant material devised by McDonald and Henderson (1964) and modified from Wylam (1953) and Harwood (1954).

Fructose and Glucose: These were estimated after separation by paper chromatography. The solvent system used consisted of ethyl acetate: pyridine: water: 10 : 4 : 3, and the evaluation was a modification of the method devised by Maurizio (1951, 1961) and Sulser (1954). Details are given in Appendix 9.

Starch: Iodine was used to test for starch (Parker, 1926).

Minerals: Approximately 2 g dried pollen was ashed in a muffle furnace at 450°C, and the calcium, magnesium, potassium, sodium, manganese and phosphorus were determined, after appropriate dilutions, using a Unicam SP 90 and a Unicam SP 900 (see Appendix 9).

Pollen Gross Energy: This was determined by using an oxygen-bomb calorimeter on mixed pollen dried at 105°C. Samples of about 0.5 g were subject to combustion in a Gallenkamp adiabatic bomb calorimeter. Corrections were made for nitrogen and sulphur.

Nucleic acid: The amount of deoxyribonucleic acid in pollens was determined using a modification of the method of Burton (1956). This was performed to discover whether the nucleic acid in these pollens was present in quantities that would affect the estimate of crude protein values based upon the formula 6.25 x N (see Appendix 9).

Amino acids: The pollen for amino acid analyses was selected from samples gathered in different years. Pollen

types were separated by macroscopic and microscopic examination and samples taken from them for dry matter determination, hydrolysis and amino acid analysis by a Technicon amino acid auto analyser using a column packed with a cationic exchange resin. The effluent from this column was pumped through a heating coil which developed a colour with the amino acids the intensity of which was recorded on a logarithmic chart, integrated by a process of triangulation for each peak and converted into an actual amount by a previously determined conversion factor (Appendix 9). For technical reasons the determination of the essential amino acid tryptophan could not be performed.

Honeybees

Samples of honeybees were collected from colonies, using an aspirator, (Bailey, 1956),and analysed for certain constituents, especially amino acids. Individual worker honeybees for analysis were randomly selected from different colonies. After their gut contents had been removed and they had been dried under vacuum at 40°C to constant weight, duplicate analyses were performed on them for nitrogen and amino acids after acid hydrolysis (see Appendix 9).

Honey

Honey cations: These were determined on dilute solutions of honey using a Unicam SP 900A. Magnesium was determined by atomic absorption and sodium, calcium and potassium by flame-photometry (see Appendix 9).

IV.9 Statistical analysis

The relationship between sites, seasons, colonies and other factors in the biological and chemical sections were examined by Student's t-test, the calculation of the correlation coefficients or analysis of variance where appropriate. Throughout this report the following convention was followed;

not significant,	p = 0.05	n.s.
significant,	p = 0.05	*
highly significant,	p = 0.01	**
very highly significant,	p = 0.001	***
standard error,	s.e.	

The probability levels are usually indicated in the results section where statistical tests have been made, but in the discussion they have been omitted for the sake of continuity. In analyses of variance the standard error of the difference between the treatment means was usually used for testing the level of significance between treatments after the variance ratio had indicated that its use was justified.

V RESULTS

The detailed results of all analyses are presented in Appendix 10. Where standard errors of treatment means or standard error of the difference between treatment means are included in tables in the Results this signifies that an analysis of variance has indicated that this is admissible. A scrutiny of the analyses of the main pollen types for the same components indicates in some cases a fair degree of variability between different pollen species but that the species composition of the different pollens was fairly consistent.

The terms "pollen stored" and "honey stored" refer to the amount of these substances present in a colony on a particular observation date.

V.1 Pollen gathering

The amount of pollen harvested by a colony of honeybees 1963-5

At Bush during these 3 seasons the mean amount of pollen trapped per colony was 1068 g, with a range from 734 to 1729 g (Table V.1).

TABLE V.1

Weight of pollen trapped by a colony 1963-5

Colony	Year	Pollen trapped (g)
X	1963	832
Y	1963	1729
F	1964	734
H	1964	760
A	1965	970
H	1965	1382
		1068 ± 167[a]

[a]Mean ± SEM

1969

In 1969 the mean amount of pollen trapped per colony was 2989 g. The mean colony harvests from the different sites are described in Table V.2

TABLE V.2

Mean colony pollen harvests for 4 sites 1969

Site	Pollen trapped (g)
Penicuik	2567
Bush	4001
Broadwood	2305
Maggie's Waas	3085
	2989 ± 617[a]

[a]Mean ± SE of difference between site means, n.s. (not significant) for p = 0.05.

Analysis of variance indicated no significant difference ($p = 0.05$) between the amounts of pollen trapped from colonies on the 4 sites. This was mainly due to the high amount of variability between the colonies which was much greater than floral differences between the sites. Colony 28 at Bush, according to the trap, collected at least double the pollen of any other colony and this contributed considerably to the high standard error between collections. If the amounts of pollen trapped monthly are compared (Table V.6) inspection shows that only in September were there significant differences between the sites: Broadwood was quite different from the others because no pollen was trapped and Maggie's Waas was significantly different ($p = 0.05$) from Bush.

The period of pollen collection

1963-5

Pollen was collected in quantity at Bush by honeybees from the middle of May for about 120 days until mid September (Table V.3).

TABLE V.3

The period of collection of main pollens 1963-5

Colony	Year	Day of year pollen harvest Began	Ended	Length of harvest
X	1963	141	256	115 days
Y	1963	141	241	100
F	1964	139	281	142
H	1964	139	233	94
A	1965	133	277	144
H	1965	133	264	131
Means		137 (17th May)	259 (16th September)	121

1969

Having examined the length of the harvesting period at Bush, it was decided to extend the observations to other sites, situated on the coast as well as inland. On all sites in 1969 the main pollen harvest began on 22nd May but it ended more rapidly on the coast, although it was only significantly shorter ($p = 0.05$) in duration at Broadwood compared with the two upland sites (Table V.4).

TABLE V.4

Main pollen collection period 1969

Site	Collection period
Penicuik	112 days
Bush	119
Broadwood	92
Maggie's Waas	105
	107 ± 5[a]

[a]Mean ± SE of the difference between site means.

The pollen harvesting pattern

1963-5

About twice as much pollen was harvested in the first half of the main pollen gathering period compared with the second half (Table V.5). The maximum rate of pollen harvesting was attained early in the season and gradually declined as the season advanced.

TABLE V.5

Pollen harvesting pattern 1963-5

Colony	Year	Mid-Season	% of pollen harvested 1st half of season	2nd half of season
X	1963	17th July	64.5	35.5
Y	1963	9th "	59.1	40.9
F	1964	27th "	70.2	29.8
H	1964	4th "	84.3	15.7
A	1965	24th "	76.8	23.2
H	1965	19th "	70.2	29.8

1969

In 1969 the pollen collecting rate was examined in greater detail (Table V.6).

TABLE V.6

Mean pollen weight trapped each month, 1969 (g)

Site	May	June	July	August	Sept.	October
Penicuik	134± 55[a]	1286±212	631± 58	378± 29	133±66	0
Bush	606±132	1841±499	863±319	532±142	93±20	0
Broadwood	249± 48	1538±227	346± 39	160± 31	0± 0	0
Maggie's Waas	294± 94	1561±237	798±159	352± 58	23±18	0
General Mean	318± 60	1557±151	659± 96	355± 49	62±21	0

[a]Mean ± SEM

Table V.6 indicates that the pollen trapped per month increased rapidly to a maximum in June and then gradually declined until October when no pollen was collected (see also Figure V.1). All 4 sites appeared to follow a similar pattern.

The honey and pollen harvests

1963-5

A comparison of the pollen harvested between 1963 and 1965 with the net weight gain of a colony in the same apiary[1] appeared to indicate that these 2 factors were inversely related (Table V.7).

[1]See Table V.33 for the relationship between net weight change and honey stored in colonies.

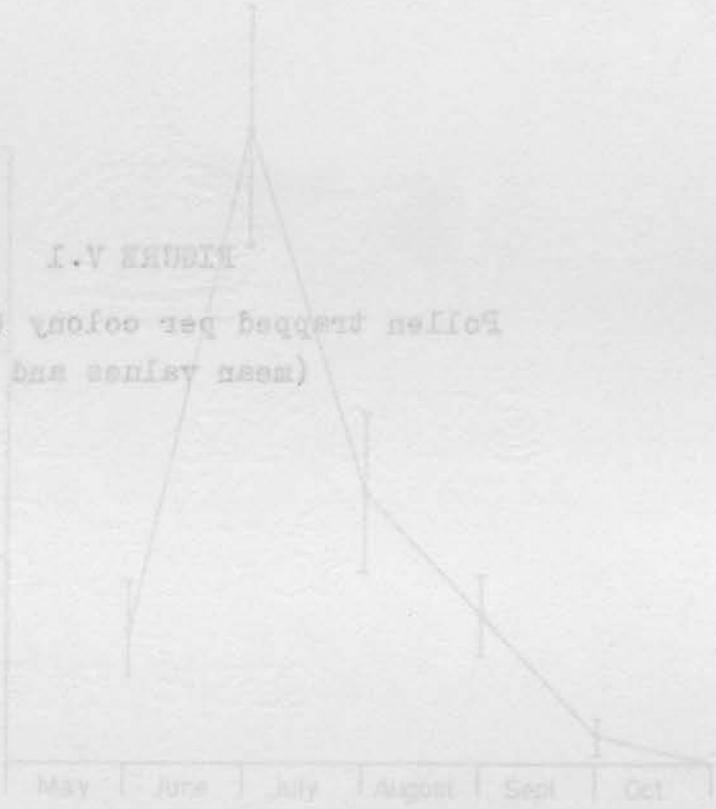

May
June
July
August
Sept
Oct

FIGURE V.1

Pollen trapped per colony (kg) per month 1969
(mean values and S.E.M.s)

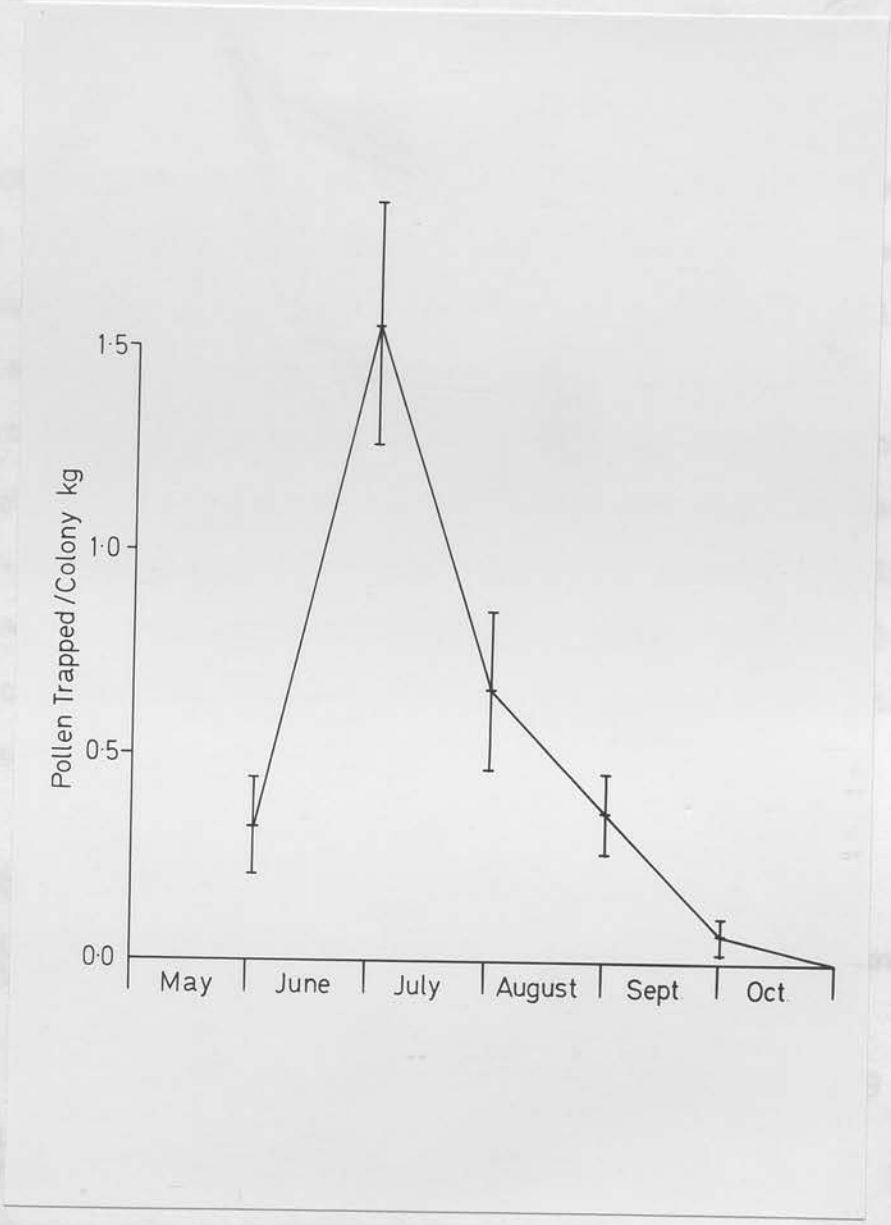

1·5
1·0
0·5
0·0
Pollen Trapped / Colony kg
May
June
July
August
Sept
Oct

TABLE V.7

Pollen gathered and colony weight gain, Bush 1963-5

Year	Total pollen trapped	Net colony weight gain
1963	2561 g	16 kg
1964	1494	50
1965	2352	17

1969

When the pollen trapped by 16 colonies in 1969 was compared with the honey stored in each of these colonies only a small non-significant ($p = 0.05$) negative correlation coefficient of $r = -0.06$ was obtained. This appeared to show that these 2 processes were unrelated. Furthermore, when they were compared on the different observation dates (Table V.8), only once, in late September, during the 1969 season was any significant correlation found ($p = 0.05$). Thus throughout the greater part of the season these phenomena were apparently unrelated.

TABLE V.8

Correlation coefficients between honey stored and pollen trapped 1969

Date	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
Correlation coefficient	0.119	0.269	-0.203	0.192	0.140	0.674
Significance	n.s.	n.s.	n.s.	n.s.	n.s.	**

The number of pollens gathered by a colony of honeybees

Between 1963 and 1965 the average number of different pollen types harvested by 2 colonies at Bush was 13. In 1969, 16 colonies on 4 different sites gathered a mean of 14 pollens (Table V.9). There was no significant difference ($p = 0.05$) between colonies on different sites, although at Bush the mean number of pollen types collected was again 13.

TABLE V.9

The number of pollens gathered by colonies in 1969

Site	Pollen types
Penicuik	14 ± 0.9[a]
Bush	13 ± 0.6
Broadwood	16 ± 1.3
Maggie's Waas	15 ± 0.6
General Mean	14 ± 0.4

[a] Mean ± SEM.

The amounts of different pollens trapped

1963-5

Between 3 and 6 pollen types in the individual colony harvests found in the traps were present in amounts greater than 5% (Appendix 3). The bulk of the pollen trapped in the 3 years considered consisted of very few types, 5 (*Acer pseudoplatanus*, Cruciferae, *Trifolium repens*, *Ranunculus* spp. and *Chamaenerion angustifolium*) represented over 85% of

the total collection (Table V.11).

1969

A similar situation was found in 1969 when observations were extended to other sites; between 3 and 7 pollen types in the individual colony harvests were present in amounts greater than 5% (Appendix 4). No differences were found between the numbers of pollens gathered on these sites in amounts greater than 5% (6 types) of the total 1969 harvest from all colonies (Table V.12) which represented 85% of the total 1969 collection (*Acer pseudoplatanus*, *Trifolium repens*, *Crataegus monogyna*, *Fagus sylvatica*, *Rubus* spp. and *Chamaenerion angustifolium*). There were no great differences between the total number of pollens collected by colonies on different sites (Table V.10).

TABLE V.10

The total number of pollen types harvested on different sites 1969

Site	No. of different pollens
Penicuik	20
Bush	21
Broadwood	24
Maggie's Waas	17
General Mean	21

TABLE V.11

The pollens trapped from 6 colonies at Bush 1963-1965
(2 colonies each year)

Pollen	Weight g	% of total harvest
Acer pseudoplatanus	2547.6	39.8
Cruciferae	1296.2	20.2
Trifolium repens	778.8	12.2
Ranunculus spp.	437.4	6.8
Chamaenerion angustifolium	399.3	6.2
Fagus sylvatica	294.6	4.6
Rubus spp.	247.3	3.9
Ericaceae	107.7	1.7
Filipendula ulmaria	82.6	1.3
Sarothamnus scoparius	64.6	1.0
Compositae	45.3	0.7
Betula spp.	36.6	0.6
Umbelliferae	34.4	0.5
Unknown	17.4	0.3
Crataegus monogyna	8.3	0.1
Vicia spp.	2.6	
Tilia vulgaris	2.3	
Caryophylaceae	2.0	
Quercus spp.	1.3	
Prunus/Pyrus	0.9	
Papaveraceae	0.3	
Plantago spp.	0.3	
Hedera helix	0.1	
Total	6407.8	

TABLE V.12

The pollens trapped from 16 colonies on 4 sites 1969

Pollen	Weight g	% of total harvest
Acer pseudoplatanus	18,062	38.0
Trifolium repens	5,514	12.0
Cruciferae	4,983	10.0
Crataegus monogyna	3,259	7.0
Fagus sylvatica	3,044	6.0
Rubus spp.	3,004	6.0
Chamaenerion angustifolium	2,916	6.0
Ranunculus spp.	1,221	2.0
Filipendula ulmaria	1,073	2.0
Compositae	942	2.0
Papaveraceae	905	2.0
Ericaceae	734	1.5
Sambucus nigra	509	1.1
Sarothamnus scoparius	310	0.7
Vicia spp.	243	0.5
Lotus corniculatus	229	0.5
Umbelliferae	192	0.4
Unknowns	160	0.3
Ulex europaeus	137	0.3
Ranunculus ficaria	108	0.2
Echium vulgare	85	0.2
Aesculus hippocastanum	68	0.1
Prunus/Pyrus spp.	63	0.1
Betula spp.	26	0.1
Allium ursinum	26	0.1
Pinus sylvestris	18	
Ligustrum vulgare	18	
Mellilotus spp.	16	
Scabiosa spp.	13	
Viola spp.	9	
Plantago spp.	2	
Campanulaceae	2	
Total	47,891	

The number of different pollens collected each month by honeybees

1963-5

The mean number of different pollen types gathered by colonies of honeybees was found to increase from 3 in May to a maximum of 9 in June, and thereafter it gradually fell to 1 type in October (Table V.13).

TABLE V.13

The number of pollen types gathered by colonies at Bush every month, 1963-5

Colony	Year	May	June	July	August	September	October
X	1963	4	10	7	6	2	0
Y	1963	4	14	7	6	0	0
F	1964	2	9	9	4	1	3
H	1964	2	7	7	5	0	0
A	1965	4	6	6	9	5	1
H	1965	3	10	7	9	4	0
Means		3	9	7	6	2	1

1969

Analysis of variance indicated that each month there was no significant difference ($p = 0.05$) between the number of pollens harvested from the colonies on the different sites (Table V.14), but when the numbers of pollens collected every month were compared with one another they were found to be significantly different ($p = 0.05$). Thus

it appeared that the time of year had a much greater effect than site upon the number of pollen types gathered by the honeybees.

TABLE V.14

The number of pollens gathered on different sites every month (1969)

	Mean number of pollen types gathered				
Site	May	June	July	August	September
Penicuik	4	5	8	5	2
Bush	4	6	8	5	2
Broadwood	3	8	11	5	0
Maggie's Waas	4	8	9	7	2
General Means	3.4	6.9	8.8	5.3	1.6 $\pm$ 0.5[a]

[a]Standard error of the difference between the monthly means

The constancy in the harvesting of different pollen types by honeybees

1963-5

Each year at Bush not only were the same few flowers utilised by the honeybees for pollen production but they were also found to be gathered in fairly similar proportions. For example sycamore, crucifer and white clover pollen were found to represent about 75% of the total pollen harvest of each colony and the pollen harvested from buttercup and rosebay willow-herb, although small, with a mean value around 13% remained fairly consistent (Table V.15).

1969

With the exception of beech no significant differences ($p = 0.05$) were found between the relative amounts of the main pollens harvested by colonies at Bush in 1963-5 compared with in 1969. It appeared then that the same pollens were being harvested from this site each season in relatively similar quantities, but pollens gathered in relatively small amounts showed stronger tendencies to be gathered in a more erratic manner (Table V.15).

TABLE V.15

A comparison of the main pollens gathered at Bush in 1963 to 1965, as percentages, with those harvested in 1969(t-test)

Pollen type	Seasons 1963-1965	Season 1969	Significance ($p = 0.05$)
Sycamore	43.0% ± 9.6[1]	38.0% ± 3.6[1]	n.s.
Crucifers	21.3 ± 5.3	9.5 ± 1.6	n.s.
White clover	10.8 ± 3.3	13.0 ± 2.6	n.s.
Buttercups	6.5 ± 1.6	4.5 ± 0.6	n.s.
Rosebay willow-herb	6.5 ± 1.9	6.3 ± 1.9	n.s.
Beech	3.5 ± 1.7	11.3 ± 2.3	*
Raspberry	3.0 ± 2.0	9.0 ± 2.3	n.s.
Totals	94.6	91.6	

[1] Mean ± SEM

The pollen preference shown by colonies of honeybees

An examination of the pollens harvested between 1963 and 1965 revealed that colonies had preferences for certain types of pollen. In 1963, for example, colony Y gathered almost twice as much beech and over three times as much buttercup pollen as colony X; examples are described in Table V.16 below.

TABLE V.16

Pollen preferences shown by colonies of honeybees 1963-5

Pollen	Year	Colony	Pollen as % of colony harvest	Colony	Pollen as % of colony harvest
Beech	1963	X	6	Y	11
Buttercups	1963	X	4	Y	14
Sycamore	1964	F	28	H	78
Crucifers	1964	F	44	H	10
Buttercups	1965	A	7	H	4
White clover	1965	A	6	H	14

In 1969 it was confirmed that differences existed in the relative amounts of the same pollens harvested on one site (Bush), and it was observed that there were also similar differences between the pollens harvested on different sites (Table V.17).

TABLE V.17

% range of pollens in colony harvest 1969

Pollens	Sites			
	Bush	Penicuik	Broadwood	Maggie's Waas
Beech	5-16	1-15	0-12	0.03-1
Buttercups	3-6	2-3	0-3	0-1
Sycamore	28-44	27-49	46-61	26-36
Crucifers	7-14	5-15	5-9	7-18
White clover	7-19	9-20	0.8-4	10-16
Rosebay willow-herb	2-11	6-14	3-6	1-7
Raspberry	6-16	0.6-13	2-6	0-2
Hawthorn	0-0.7	0.2-3	2-20	12-28

Variations in the amount of important pollens[1] harvested at different sites in 1969

An analysis of variance of the relative amounts of the more important pollens harvested from the 4 different sites indicated that only crucifer and rosebay willow-herb pollens, which represented 16% of the total harvest in 1969, were harvested in similar amounts at the different sites.

The Broadwood site harvest contained significantly more sycamore and less white clover ($p = 0.05$), while Maggie's Waas harvest had significantly less beech and Rubus spp. pollen ($p = 0.05$). Penicuik and Bush contained significantly less hawthorn ($p = 0.05$), (Table V.18).

[1] That is pollens representing more than 5% of the total harvest in 1969.

TABLE V.18

A comparison of the % harvest of important pollens on different sites in 1969

Pollen	Sites				
	Penicuik	Bush	Broadwood	Maggie's	Waas
Sycamore	33.0%	38.0	54.0	32	± 5.2[a]
White clover	16.0	13.0	2.2	13	± 2.8
Crucifers	12.0	10.0	7.0	11	± 2.7
Hawthorn	1.6	0.2	9.5	18.8	± 3.6
Beech	8.3	11.3	3.1	0.5	± 3.6
Rubus spp.	7.9	9.0	4.5	0.8	± 2.6
Rosebay willow-herb	11.0	6.0	4.0	5.0	± 2.3

[a]S.E. of the difference between site means.

The seasonal distribution of pollen sources

1963-5

The main pollens[1] were trapped during the periods indicated in Table V.19. There was a large variation in the trapping periods ranging from 5 days for broom to 94 days for crucifers.

[1]Pollens representing more than 1% of the total 3 years' harvest.

TABLE V.19

Mean trapping times of main pollens, 1963-5

Pollens	Mean trapping time		Length (days)
	Began	Ended	
Beech	18 May	30 May	12
Broom	21 June	27 June	5
Buttercups	19 June	26 July	37
Crucifers	6 June	7 September	94
Heaths	28 June	30 August	65
Meadow sweet	7 July	11 August	35
Raspberry	9 June	26 June	18
Rosebay willow-herb	21 July	10 September	52
Sycamore	16 May	18 June	33
White clover	25 June	2 September	70

1969

In 1969 the pollen harvesting times ranged from 1 day for buttercup, meadow sweet and hawthorn to 114 days for composites and crucifers (Table V.20).

TABLE V.20

The trapping times of the main pollens[1] 1969

Pollens	Harvest period		Length (days)
	Began	Ended	
Beech	26.5-5.6	3.6-25.6	8-20
Buttercups	25.6-3.7	12.6-17.9	1-76
Composites	26.5-25.7	25.7-17.9	21-114
Crucifers	26.5	25.7-17.9	60-114
Meadow sweet	9.7-14.8	7.8-22.8	1-44
Hawthorn	3.6-23.6	23.6-25.6	1-22
Poppy	26.5-25.6	25.7-22.8	30-60
Rosebay willow-herb	17.7-25.7	22.8-18.9	28-55
Rubus spp.	6.6-11.6	25.6-30.7	17-52
Sycamore	26.5	13.5-18.5	18-23
White clover	12.6-13.7	22.8-18.9	71-81

[1]Pollen representing more than 1% of the total harvest.

The effect of land use on the pollens collected 1963-5

The land for 1,000 metres around the site at Bush House was examined during 1963, 1964 and 1965; it was covered with meadow, arable and mixed woodland in the relative proportions of approximately a half, a third and a fifth of the area considered. The mean situation is described in Table V.21.

TABLE V.21

Land use within 1,000 m of Bush House site, 1963-5

Habitat	% of total area
Arable	29.0
Meadow	42.8
Mixed woodland	19.4
Coniferous woodland	4.5
Roads, buildings and water	4.3
Total	100.0

The floral sources of the pollens harvested by the honeybees were classified according to habitat in Table V.22.

TABLE V.22

The main pollens collected in 1963-5 and associated habitats

Habitat	Pollens
Arable	Crucifers
Meadow	Buttercup, composites, heaths, meadow sweet, pinks, vetches and white clover.
Mixed woodland	Beech, broom, fruit trees, hawthorn, lime, oak, raspberry, sycamore and rosebay willow-herb

Pollens harvested from each colony were classified into the habitats from which they originated in Table V.23.

TABLE V.23

Mean % of pollen harvested from each habitat, Bush 1963-5

Habitat	Mean % of pollen harvest	S.E.M.[1]
Arable	21.5	± 5.28
Meadow	20.6	± 4.27
Mixed woodland	57.9	± 7.32
Total	100.0	

[1]Standard error of the mean.

The greatest amount of pollen, over half the total, was collected from mixed woodland, while the arable and meadowland habitats each produced about 20%. The percentage of pollen harvested from each of these habitats lying within 1,000 metres of the colonies was calculated on a per unit area basis[1] (Table V.24).

TABLE V.24

Ratio of % pollen harvested from various habitats and % areas occupied by habitats, Bush 1963-5

Habitat	
Arable	0.74 ± 0.18[a]
Meadow	0.47 ± 0.09
Mixed woodland	2.98 ± 0.38

[a]Mean ± SEM.

[1]That is the percentage of the total pollen harvested from each habitat was divided by the percentage of the total area within 1,000 m of the site occupied by that habitat.

Relatively more pollen was harvested by honeybees from a unit of woodland than from an equivalent area of either arable or meadowland, and of the latter two, arable habitats appeared to be more valuable to honeybees for pollen production. Arable-habitat pollens were mostly derived from crucifers, meadow pollens were predominantly harvested from white clover and buttercup, and in mixed woodland, sycamore, beech tree, raspberry and rosebay willow-herb pollens were the most important.

In 1969 these phenomena were examined on other sites besides Bush. The land use of the area within 1,000 metres of each site was determined (Table V.25).

TABLE V.25

% of land use within 1,000 m of the sites 1969

Habitat	Sites				
	Penicuik	Bush	Broadwood	Maggie's	Waas
Arable	14.3	29.0	13.7	83.0	35.0 ± 16.4[b]
Meadow	34.4	42.8	37.0	1.5	28.9 ± 9.3
Mixed woodland	37.1	19.4	28.0	12.5	24.3 ± 5.3
Coniferous woodland	7.7	4.5	10.8	0.0	5.8 ± 2.3
Roads, buildings, and water	6.5	4.3	10.5	3.0	6.1 ± 1.6
Totals	100.0	100.0	100.0	100.0	

[b] Mean ± SEM.

In addition the percentage of pollen produced from each habitat was also calculated (Table V.26).

TABLE V.26

% of the pollen harvest for each site collected from each habitat 1969

	Sites				
Habitat	Penicuik	Bush	Broadwood	Maggie's	Waas
Arable	11.5	9.7	15.7	11.7	12.1 ± 3.0[a]
Meadow	26.1	24.3	6.6	28.5	21.4 ± 1.8
Mixed woodland	62.4	65.9	77.7	59.8	66.5 ± 4.1
Coniferous woodland	0.0	0.1	0.0	0.0	0.0 ± 0.0
Totals	100.0	100.0	100.0	100.0	

[a]Site means and standard error of the difference between site means.

This indicated that although the harvest of pollen from these different habitats was variable, woodland, then arable and finally meadow plants were relatively the most important sources of pollens for honeybees. No significant differences ($p = 0.05$) existed between the relative amounts of arable, meadow or mixed woodland pollens harvested from the different sites except for Broadwood where significantly more mixed woodland and significantly less ($p = 0.05$) meadow pollen was gathered. Much more pollen was produced per unit area of woodland than from arable or meadowland which were both very similar (Table V.27). On the Maggie's Waas site the relative production of meadow pollen per unit area

was very high.

TABLE V.27

Ratio of % of the pollen harvest from various habitats and % areas occupied habitats[1] 1969

Habitats	Sites				
	Penicuik	Bush	Broadwood	Maggie's	Waas
Arable	0.68	0.40	1.15	0.15	0.60 ± 0.21[a]
Meadow	0.71	0.61	0.18	19.13	0.50 ± 0.16[b]
Mixed woodland	1.78	3.20	2.78	4.80	3.14 ± 0.63

[1] See Experimental section

[a] Mean ± SEM

[b] Maggie's Waas was omitted from this calculation of the mean because it was very atypical.

V.2 The effect of pollen traps upon colonies of honeybees

The observations of the adult honeybees, brood, honey stored and pollen stored from the trapped and untrapped colonies for each of the seven dates in the 1969 season (see Appendix 7) were transformed into the equivalent natural logarithms. Variances and means were calculated and aggregated for each group, and significant differences established ($p = 0.05$) using the appropriate calculated critical difference to compare the means. Differences between trapped and untrapped colonies were significant ($p = 0.05$) in only 4 of the 24 sets of data (see Table V.28) and in 3 of these cases

TABLE V.28

A comparison between the numbers of adult honeybees, and brood, and the amount of honey and pollen stored in colonies with and without pollen traps[1]

	Dates						
	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
Adult honeybees							
Trapped mean (16)[a]	17,706	17,644	23,659	37,225	37,419	17,531	13,419
Untrapped mean (7)	15,325	20,386	22,114	33,057	32,929	21,557	14,314
Significance	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Brood							
Trapped mean (15)	13,343	19,786	21,152	18,561	16,227	7,409	604
Untrapped mean (5)	9,678	24,178	22,282	20,838	19,660	8,312	879
Significance	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Honey stored (g)							
Trapped mean (16)	6,812g	5,550	11,326	15,247	13,942	15,589	17,983
Untrapped mean (7)	7,153	7,457	15,953	16,297	14,191	16,717	21,123
Significance	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.
Pollen stored (g)							
Trapped mean (16)	1,064	1,332	2,740	1,863	1,631	1,741	1,015
Untrapped mean (7)	707	1,271	3,589	2,304	1,903	2,256	1,147
Significance	*	n.s.	*	n.s.	n.s.	n.s.	n.s.

[a]The number of colonies included in each mean are indicated in parenthesis

[1]Pollen traps were fitted to colonies on the 22nd of May.

the observations from the trapped, as opposed to the untrapped colonies, were significantly less. The pollen and honey stored in the trapped colonies were less in mid-June and the adult honeybee populations were smaller in late August. On the 21st of May the colonies to which traps were to be fitted had significantly more ($p = 0.05$) pollen in store than the others. Although the differences between the trapped and the untrapped colonies during 1969 were very few, when the colonies were examined again in the spring of 1970, 30% of the trapped colonies had died compared with only 13% of the untrapped ones (Table V.31).

V.3 Some effects of environmental variation on colonies of honeybees

Adult honeybee population

The annual adult bee populations of the colonies reached their maximum in late June and early July, and then declined fairly rapidly (Table V.29). Although the coastal colonies were initially much less populous than those sited inland, they rapidly increased their numbers until there was no significant difference between the colonies in the two habitats. In late August the bee populations of the inland colonies again became significantly larger than those of the coastal colonies (Table V.29).

Brood reared

The amount of brood reared by all the colonies increased rapidly until mid-June and thereafter fell to a very low

Note. In Table V.29 below:

[1] Comparisons were performed using the natural logarithmic transformations of the raw data and statistical methods similar to those used to determine the effect of pollen traps on colonies of honeybees.

[2] The comparison between the means of the pollen trapped by colonies was performed on untransformed data by a simple t-test.

[a] The number of colonies included in each mean is indicated in parentheses.

[b] The means dated 4th June are for pollen collections beginning on the 22nd May.

TABLE V.29

Comparison between colonies of honeybees on inland and coastal sites 1969[1]

	Dates						
	29.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
Adult honeybees							
Inland means (12)[a]	22,183	19,667	23,142	33,317	34,492	20,317	14,583
Coastal means (11)	12,868	16,909	23,240	38,836	36,758	17,683	13,158
Significance	*	n.s.	n.s.	n.s.	n.s.	*	n.s.
Brood							
Inland means (10)	12,229	21,252	21,947	20,355	19,419	11,383	1,313
Coastal means (10)	12,625	20,516	20,922	18,287	14,752	3,887	32
Significance	n.s.	n.s.	n.s.	n.s.	n.s.	*	*
Honey stored (g)							
Inland means (12)	7,231	4,108	10,203	14,555	14,567	20,307	27,430
Coastal means (11)	7,881	8,337	15,496	16,659	13,419	11,159	9,675
Significance	n.s.	*	*	n.s.	n.s.	*	*
Pollen stored (g)							
Inland means (12)	610	770	2,168	1,521	1,250	1,737	882
Coastal means (11)	1,113	1,123	3,108	1,961	1,769	1,353	920
Significance	n.s.	*	n.s.	n.s.	n.s.	*	n.s.
Pollen trapped[2](g)							
Inland means (8)	-	727[b]	886	348	194	1,017	113
Coastal means (8)	-	640	854	357	212	609	11
Significance		n.s.	n.s.	n.s.	n.s.	n.s.	*

level in late September (Table V.29). Brood rearing was significantly less in coastal colonies towards the end of the season in late August and in September (Table V.29).

Honey stored

Honey stored by the inland colonies decreased until the first nectar flow in early June when it began to increase and continued to rise until the end of the season. In the coastal area the quantity of stored honey increased until mid-June thereafter falling rapidly at first and then more slowly (Table V.29). Significantly more honey ($p = 0.05$) was stored from the early season nectar flow by the coastal colonies and from the late flow of August and September by those on inland sites (Table V.29).

Pollen stored

The pollen stored increased to a peak in mid-June and then gradually fell towards the end of September to approximately the quantity found in the colonies when observations began in May (Table V.29).

Pollen trapped

The mean pollen obtained by trapping of honeybee colonies throughout the season followed a similar pattern in both the coastal and upland sites (Tables V.29 and 30) rising rapidly to a mid-June peak, declining to a fairly low rate in late June, and finally almost ceasing altogether in late September. Significantly more pollen ($p = 0.05$) was trapped inland compared with at the coasts only in late September (Table V.29).

The mean pollen trapping rates per day were calculated in Table V.30 to examine the pollen trapping situation in greater detail and so clarify whether the conclusions reached from the observations as arranged in Table V.29 were valid.

TABLE V.30

Mean pollen trapping rates (g per day) of honeybee colonies 1969

Period from	22 May	4 June	11 June	23 June	7 July	20 Aug.
to	4 June	11 June	23 June	7 July	20 Aug.	9 Sept.
Inland sites (8)[a]	56	127	29	14	23	3
Coastal sites (8)	49	122	30	15	14	0

[a]Figures in parenthesis indicate the number of colonies contributing to each mean.

Wintering

Although there was significantly less brood reared in the coastal colonies towards the end of the season in late August and in September this had no effect on the winter survival rate because when the colonies were inspected in the spring of 1970 the death rate had been 25% in each case (Table V.31).

TABLE V.31

The condition of the colonies in April 1970

Colony	Site	Condition
9	Penicuik (T)[1]	Weak[3]
38		Strong[4]
39		Weak
11		Strong
19	Bush (U)[2]	Weak
3		Dead
37		Strong
31		Weak
50	Bush (T)	Dead
32		Strong
25		Dead
28		Strong
8	Broadwood (U)	Strong
53		Weak
36		Strong
44		Weak
13	Broadwood (T)	Weak
27		Dead
56		Strong
51		Weak
48	Maggie's Waas (T)	Strong
12		Dead
30		Dead
35		Weak

[1]Trapped colonies [2]Untrapped colonies

[3]Less than 6 frames covered with honeybees

[4]Six or more frames covered with honeybees

V.4 Seasonal changes in colonies of honeybees and relationships between important colony properties[1]

Adult honeybees

The adult honeybee population in the colonies increased rapidly from about 18,000 in late May to a maximum of nearly 38,000 individuals in mid-summer, and then declined rapidly until the mean population per colony was just over 13,000 in late September (Figure V.2).

Brood

The trends in brood populations (eggs, larvae and pupae; Figure V.3) were rather similar to those of the adults, (Figure V.2) although the latter were over a fortnight later in reaching their maxima. The relationship between brood and adult bees is complex; in the growth phase of both populations there was a very significant ($p = 0.01$) positive relationship (Table V.32). However, by 23rd June when the adult population was nearly at its peak, the brood had already begun to decline, and the correlation between these two factors was no longer significant ($p = 0.05$), but by 7th July a significant ($p = 0.05$) negative correlation between brood and adult bees became apparent, indicating that the decline of brood was inversely related to the adult population size. An examination in late August indicated that there was again apparently a relationship between the declining brood and bees although it was just below the level of significance ($p = 0.05$) to the amount of brood being

[1] These data were obtained from 16 trapped colonies.

FIGURE V.2

Honeybees per colony 1969 (mean values and S.E.M.s)

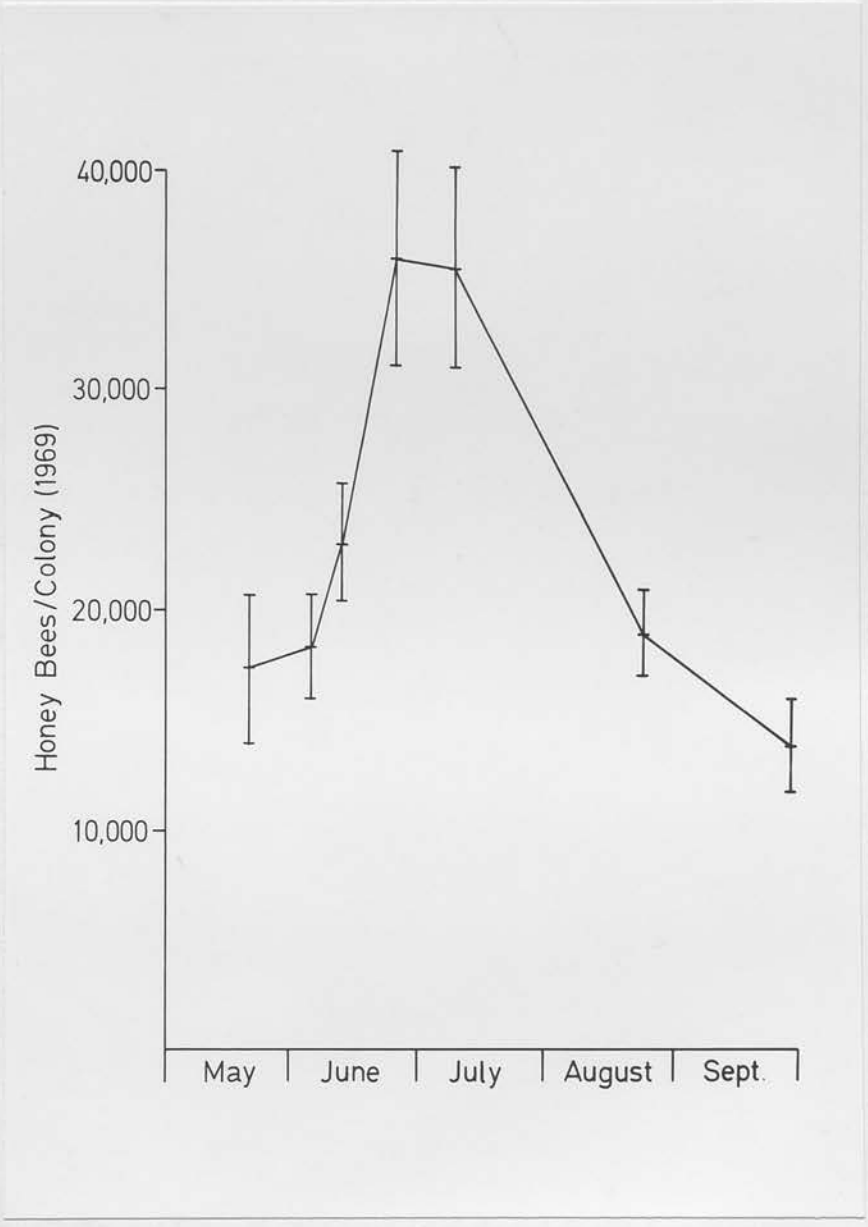
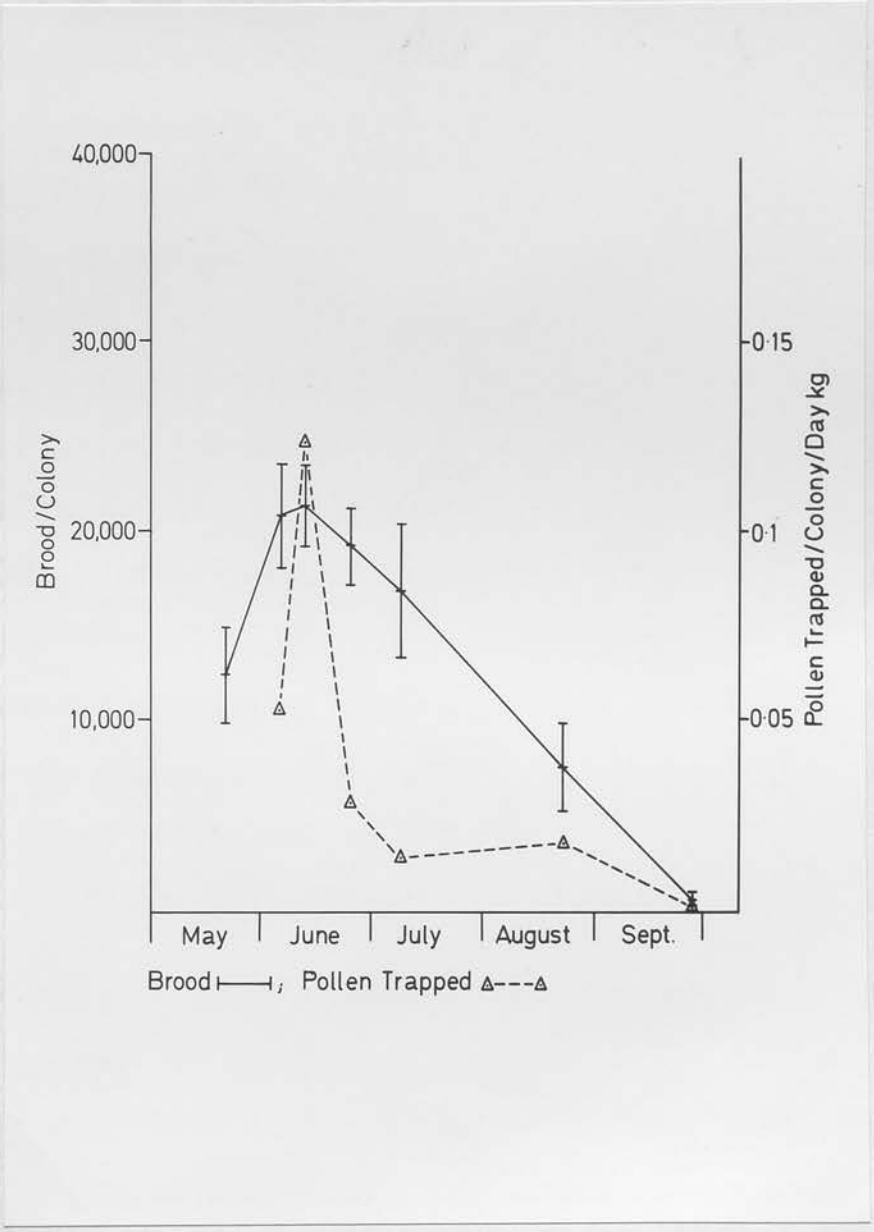

40,000
30,000
20,000
10,000
Honey Bees/Colony (1969)
May
June
July
August
Sept.

FIGURE V.3

Mean brood and S.E.M.s compared with pollen trapped per colony per day, 1969


40,000
30,000
20,000
10,000
Brood/Colony
0·15
0·1
0·05
Pollen Trapped/Colony/Day kg
May
June
July
August
Sept.
Brood ⊢—⊣; Pollen Trapped △---△

reared at this stage.

It should be noted that in mid-summer a few colonies were found to have reduced their brood as if making preparations for swarming.

Pollen trapped and pollen stored

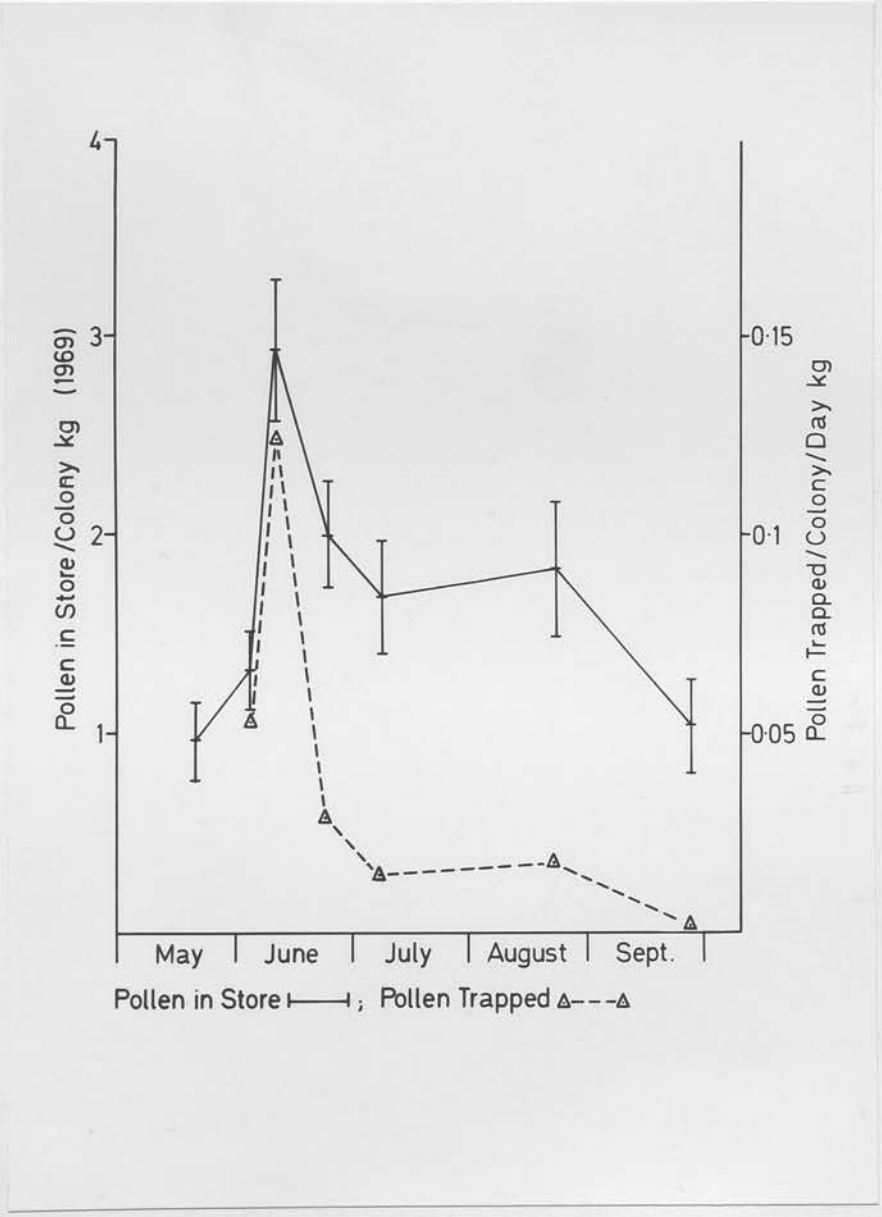
The amounts of pollen trapped per day and stored (Figure V.4) in the colonies followed a fairly similar pattern, increasing to a maximum in early June, gradually declining in early July, increasing again in August and decreasing finally in September. The correlation coefficients for pollen trapped with pollen stored did not however approach significance (Table V.32), and the relationship between the pollen trapped and the brood reared did not become significant ($p = 0.05$) until very late in the season, although an examination of the rate of pollen trapping indicated that it followed a fairly similar pattern to that of the brood (Figure V.3). However the colonies' mean brood numbers were significantly correlated ($p = 0.05$) with the colonies' mean pollen trapped per day ($r = 0.63$) and the mean pollen in store per colony ($r = 0.56$).

Honey

The amount of honey stored in the colonies in 1969 followed the pattern already established for this area in the study of nectar flows in the South-East of Scotland (Figure V.5). There was an increase in honey from the 2 nectar flows, in spring and late summer. At other times the amount of honey in store declined because it was being used for colony

FIGURE V.4

Mean pollen in store per colony and S.E.M.s compared with pollen trapped per colony per day, 1969


4
3
2
1
Pollen in Store/Colony kg (1969)
0·15
0·1
0·05
Pollen Trapped/Colony/Day kg
May
June
July
August
Sept.
Pollen in Store ⊢—⊣ ; Pollen Trapped △---△

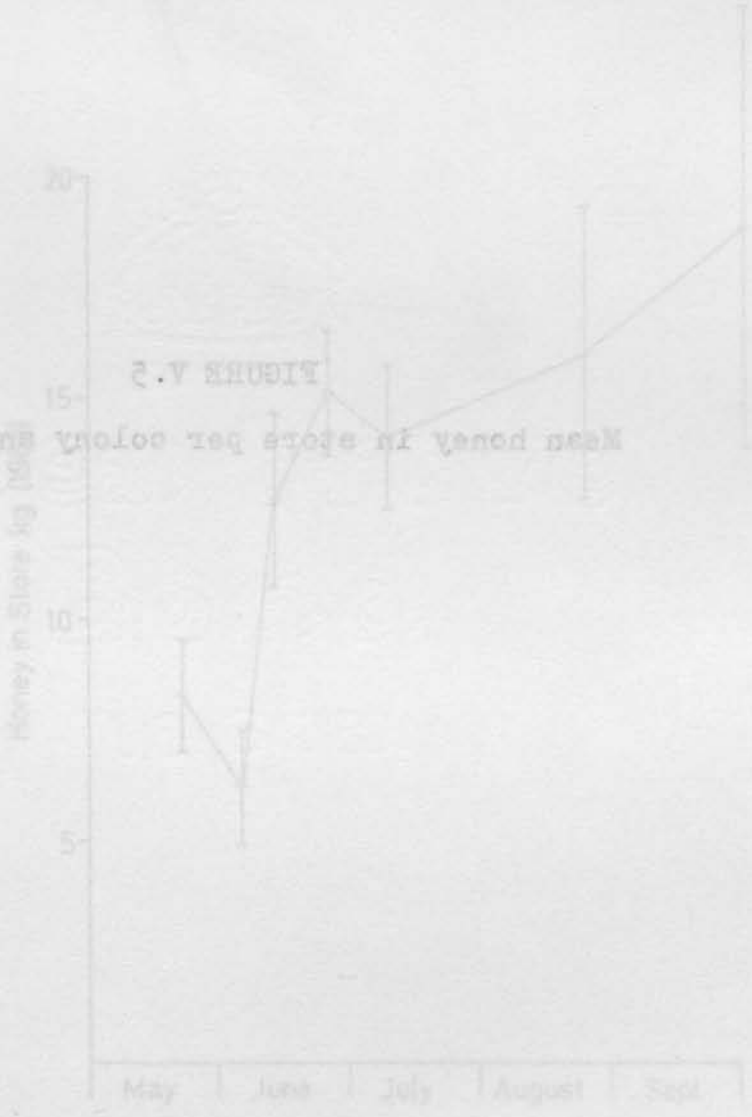

20
15
10
5
May
June
July
August
Sept

FIGURE V.5

Mean honey in store per colony and S.E.M.s, 1969

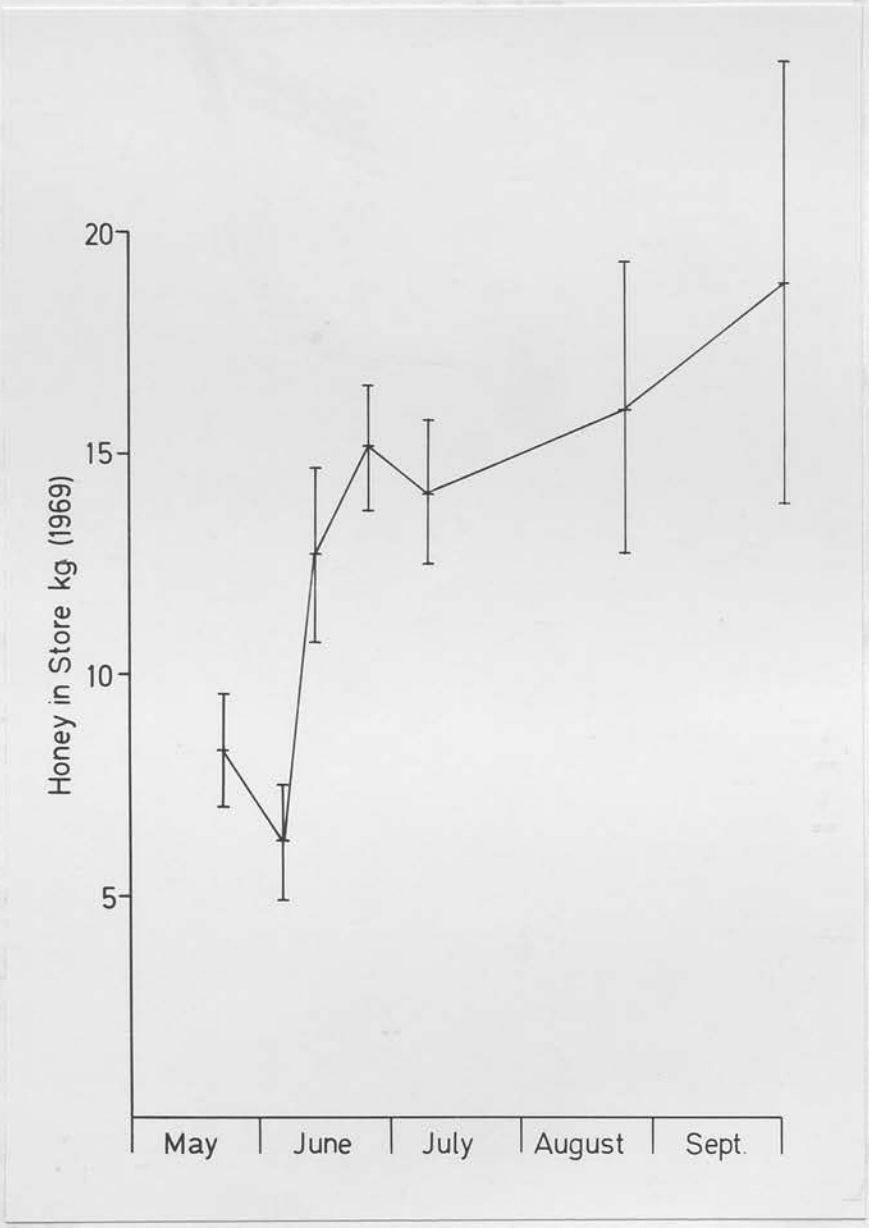

Honey in Store kg (1969)
20
15
10
5
May
June
July
August
Sept.

TABLE V. 32

An examination of the relationship between honey stored, pollen trapped, pollen stored, brood and adult honeybees by a multi-regression correlation matrix [1,2]

	Pollen trapped	Honey stored	Bees	Brood
Date: 4.6.69				
Honey stored	0.119			
Bees	- 0.256	- 0.357		
Brood	- 0.146	- 0.506*	0.801***	
Pollen stored	0.223	0.640**	- 0.034	- 0.219
Date: 11.6.69				
Honey stored	0.269			
Bees	- 0.082	0.135		
Brood	- 0.241	0.165	0.884***	
Pollen stored	- 0.320	0.113	0.187	0.193
Date: 23.6.69				
Honey stored	- 0.203			
Bees	- 0.110	0.494		
Brood	0.132	0.083	0.338	
Pollen stored	0.329	- 0.092	0.030	0.236
Date: 7.7.69				
Honey stored	0.192			
Bees	- 0.318	0.371		
Brood	- 0.076	- 0.627**	- 0.499*	
Pollen stored	0.258	0.331	0.157	0.237
Date: 20.8.69				
Honey stored	0.140			
Bees	0.231	0.361		
Brood	0.411	0.104	0.477	
Pollen stored	0.079	0.768***	0.561*	0.247
Date: 23.9.69				
Honey stored	0.674**			
Bees	0.307	0.530*		
Brood	0.500*	0.520*	0.337	
Pollen stored	0.317	0.581*	0.104	0.024

[1] Calculated on log (x + 1) transformations of the raw data

[2] Data from 16 colonies for each date.

maintenance (Table V.32); the only time when there was a significant ($p = 0.05$) positive relationship between bees base and honey stored was in September.

V.5 Nectar Flows

The relationship between honey stored and colony weight[1]

The relationship between honey stored and the net weight of 16 colonies was examined in 1969 throughout the active season. A very close relationship was found between these two variables as the mean correlation coefficient, $r = 0.95^{***}$ showed (Table V.33 and Appendix 6). Total net colony weight could thus be used as an indication of the fluctuations in the amount of honey stored in a colony, and would therefore be useful in the study of nectar flows.

TABLE V.33

The correlation between honey stored and total net colony weight for 16 colonies of honeybees 1969

Date:	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
r	0.942^{***}	0.874^{***}	0.898^{***}	0.937^{***}	0.950^{***}	0.988^{***}	0.998^{***}

The nectar flows of coastal and upland areas in the East of Scotland

The coastal colonies exhibited a consistent pattern of net weight change (Table V.34; Figures V.6, 10, 11 and 12; Appendix 6). This was characterised by a single good regular nectar flow which occurred at the beginning of each

[1] Colony represents the honeybees, brood, honey and pollen stored in this context.

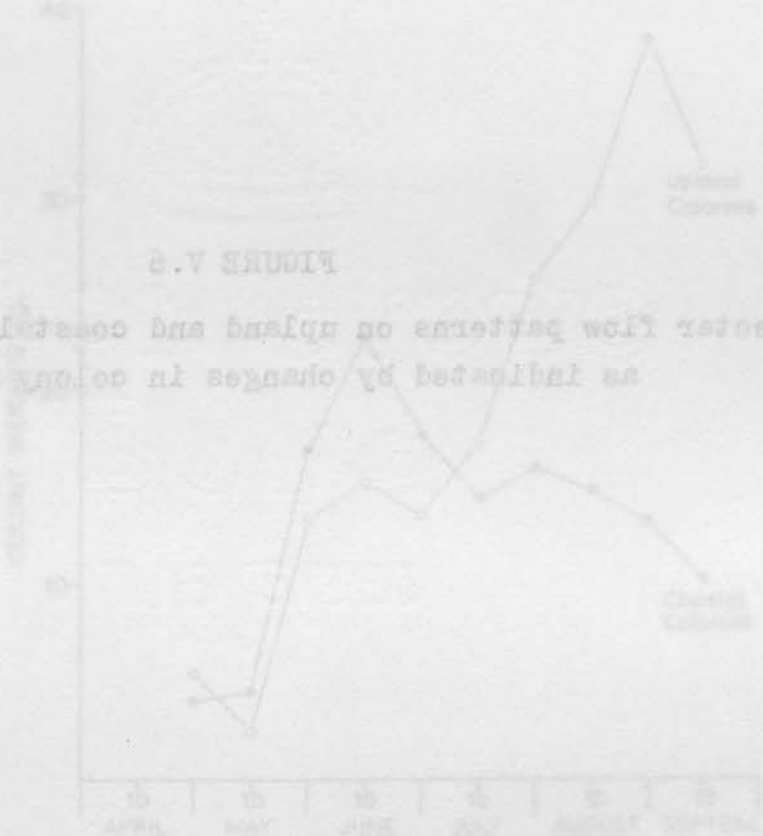
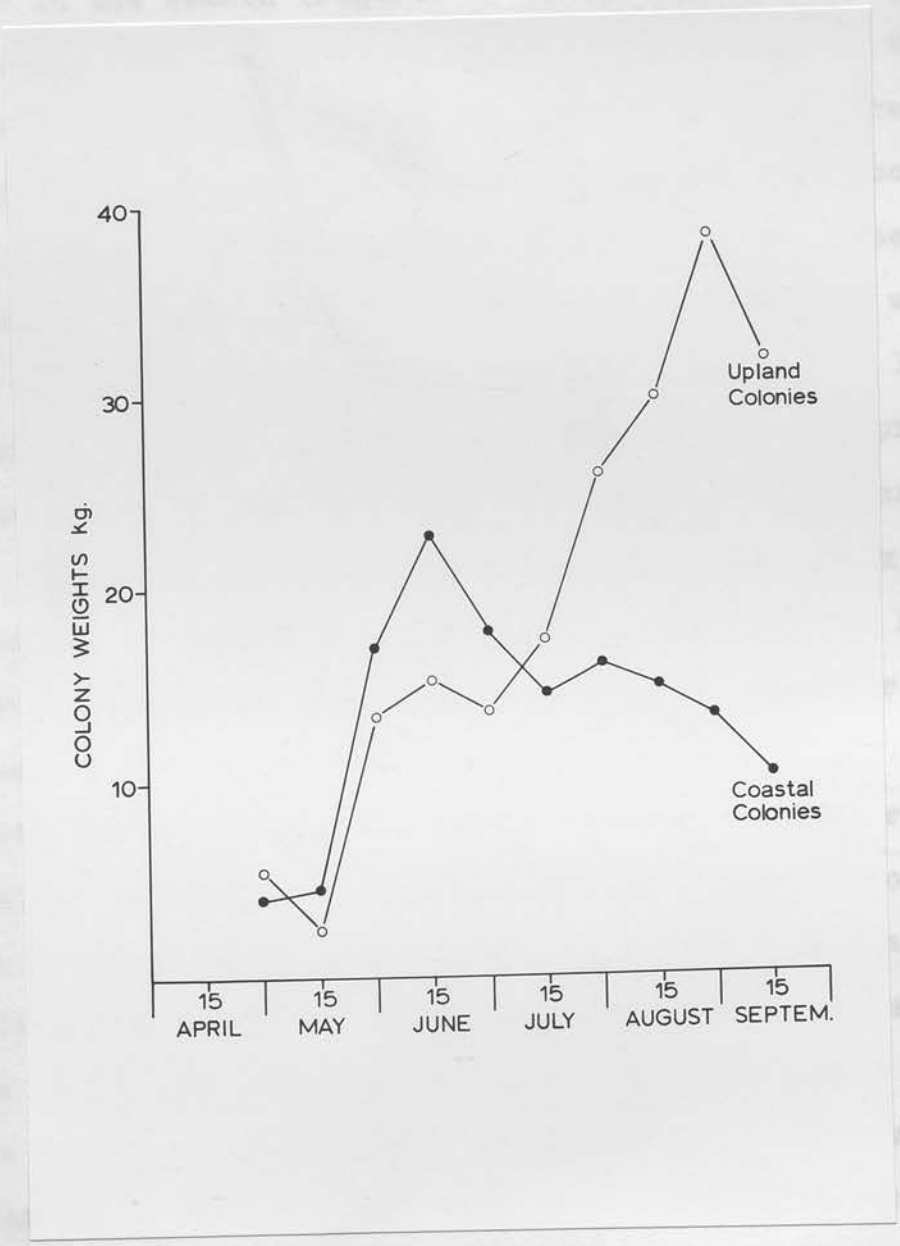


FIGURE V.6

Nectar flow patterns on upland and coastal sites 1964-1966
as indicated by changes in colony weights


40
30
20
10
COLONY WEIGHTS kg.
Upland Colonies
Coastal Colonies
15 APRIL
15 MAY
15 JUNE
15 JULY
15 AUGUST
15 SEPTEM.

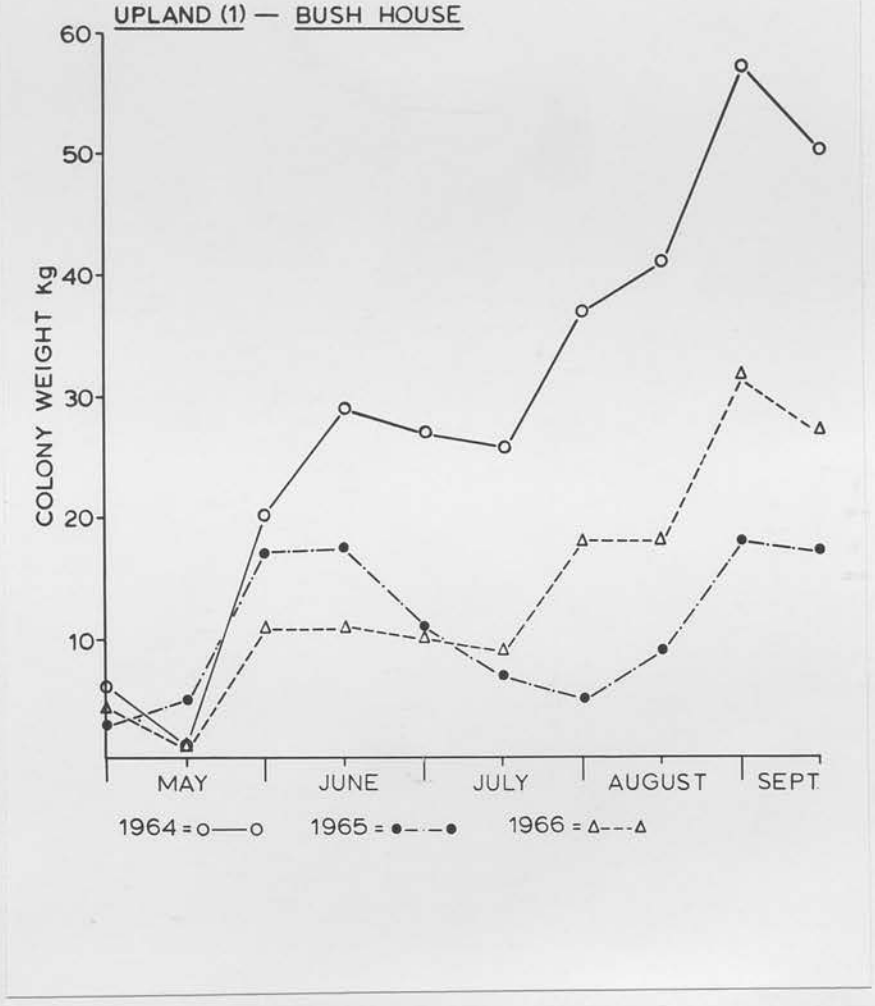
season between mid May and early June. It appeared to be mostly gathered from sycamore trees which grow well there. A second but much smaller nectar flow was also noted between July and early August.

In the upland areas, 3 different nectar flows appeared to occur in the season (Figures V. 6, 7, 8 and 9). The first nectar flow was observed regularly each year in the May-June period and was, as in the coastal area, apparently obtained from sycamore. A second good nectar flow occurred in July from various combinations of white clover, rosebay willow-herb, bell heather and lime trees. This flow was erratic and could not be relied upon every year. In 1965 for example there was no evidence of its occurrence; probably this was caused by the generally poor weather conditions in July. The third and final nectar flow was noted from the ling heather in August each year, indicating that the honey-bees were prepared to fly further than normal (Beutler, 1954) when there was no other source of nectar.

Both the upland and the coastal colonies showed regular seasonal variations in weight (Table V.34), but the coastal pattern appeared to be consistemtly different from that of the upland area. These differences became more marked towards the end of each season except in 1965. When observations from the coastal sites were aggregated and compared with similarly arranged data from the upland sites throughout the season, it was observed that there was a tendency for the coastal colonies to store more honey earlier but this was completely reversed by the end of each season (Figure V.6).

FIGURE V.7

Nectar flows at Bush House 1964-1966 as indicated by changes in honeybee colony weights


UPLAND (1) — BUSH HOUSE
COLONY WEIGHT Kg
60
50
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT
1964 = o—o
1965 = ●–·–●
1966 = Δ---Δ

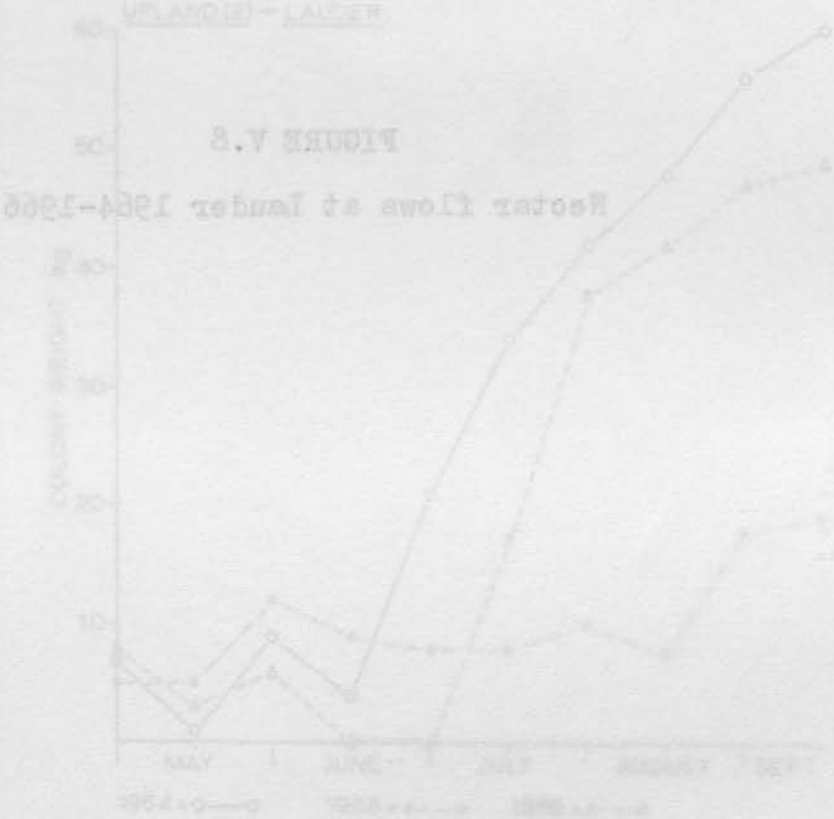
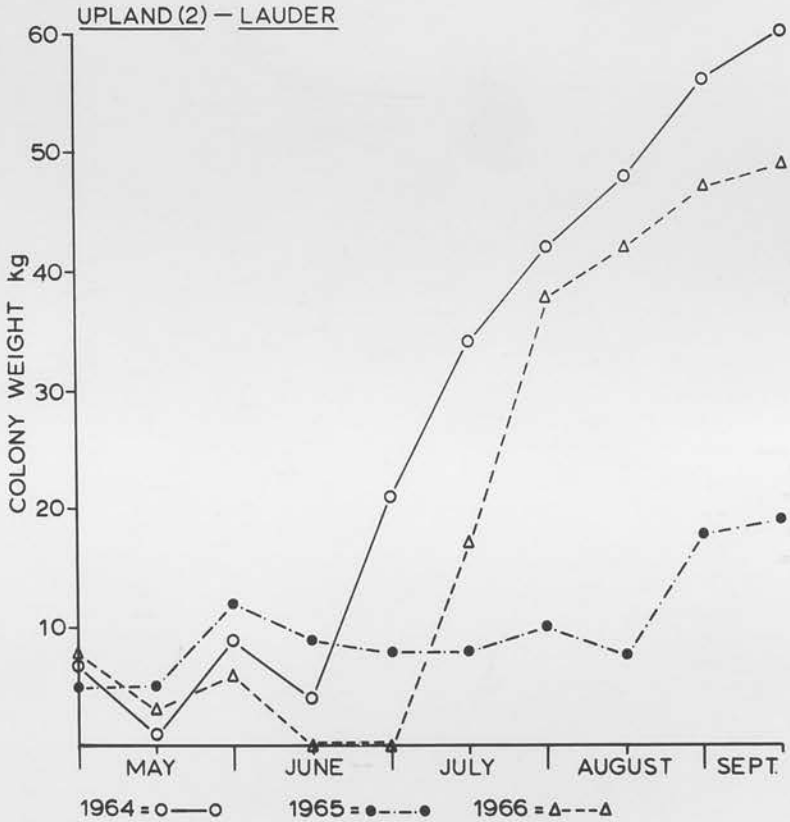


FIGURE V.8

Nectar flows at Lauder 1964-1966


UPLAND (2) — LAUDER
COLONY WEIGHT kg
60
50
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT.
1964 = o—o
1965 = ●-·-●
1966 = Δ---Δ

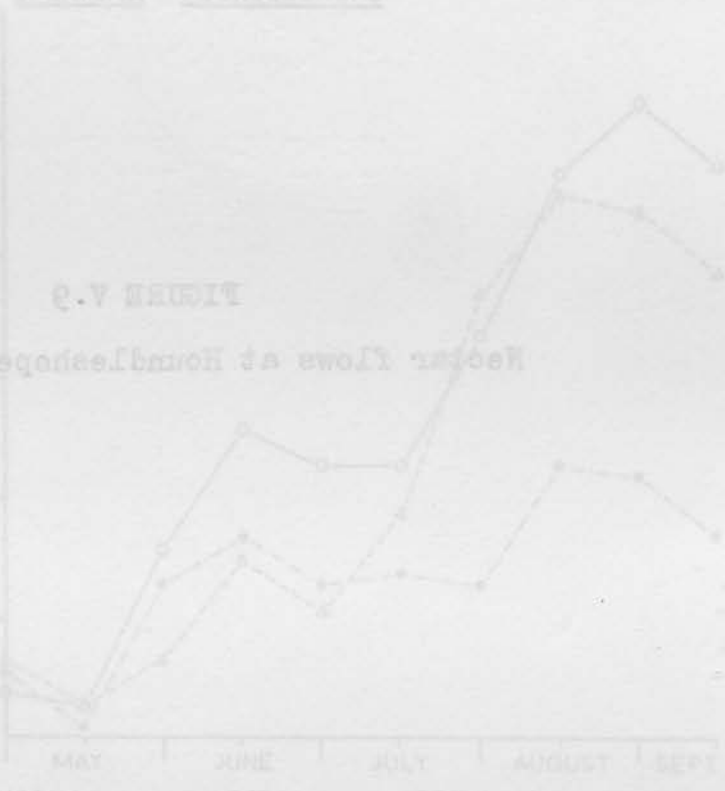
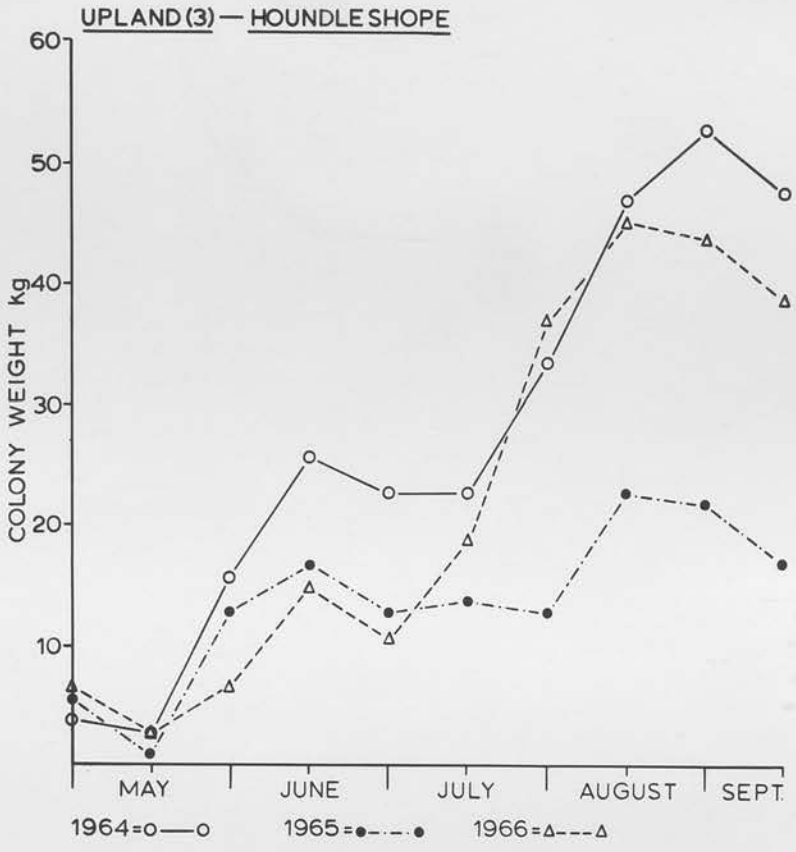

MAY
JUNE
JULY
AUGUST
SEPT

FIGURE V.9

Nectar flows at Houndleshope, 1964-1966


UPLAND (3) — HOUNDLE SHOPE
COLONY WEIGHT kg
60
50
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT.
1964 = o — o
1965 = ● - · - ·
1966 = Δ - - - Δ

JUNE
JULY
AUGUST
SEPT

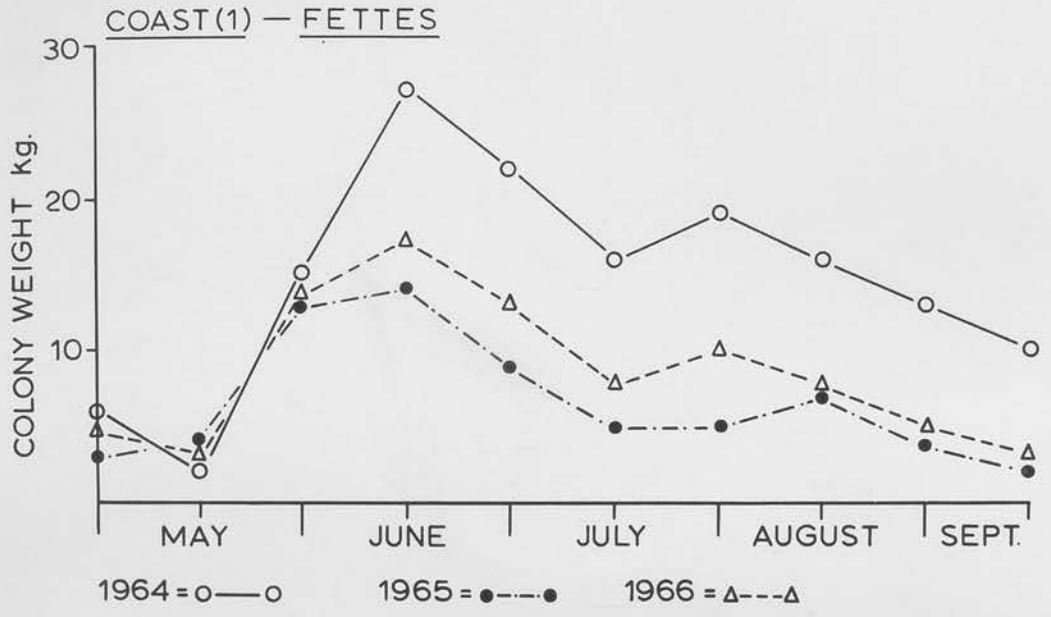
JUNE
JULY
AUGUST
SEPT

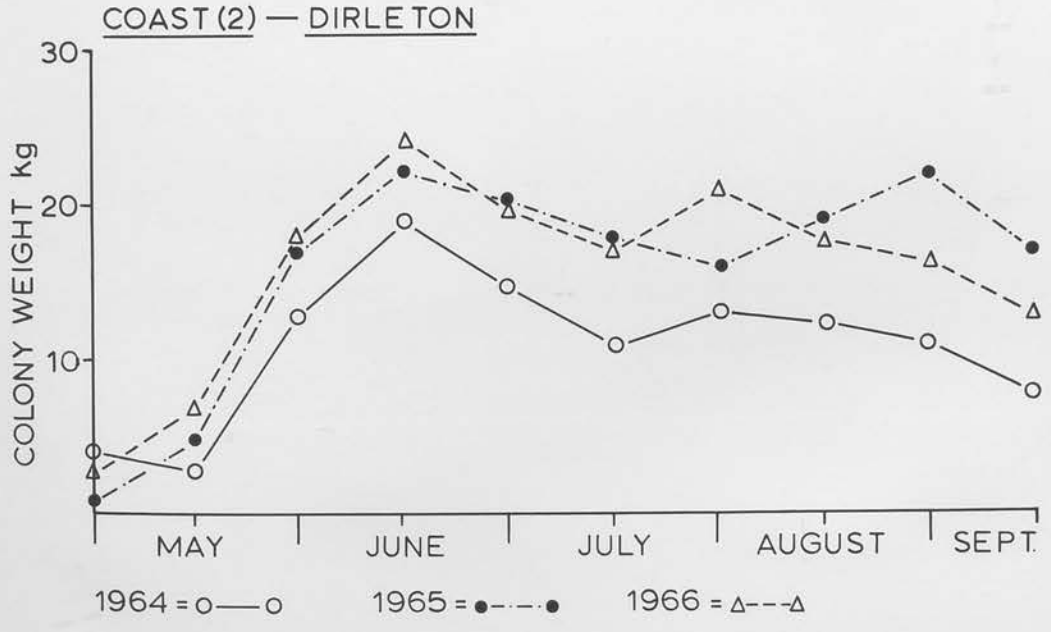
FIGURE V.10

Nectar flows at Fettes 1964-1966

FIGURE V.11

Nectar flows at Dirleton 1964-1966


COAST (1) — FETTES
COLONY WEIGHT Kg.
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT.
1964 = o—o
1965 = ●-·-·●
1966 = Δ---Δ


COAST (2) — DIRLETON
COLONY WEIGHT kg
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT.
1964 = o—o
1965 = ●-·-·●
1966 = Δ---Δ

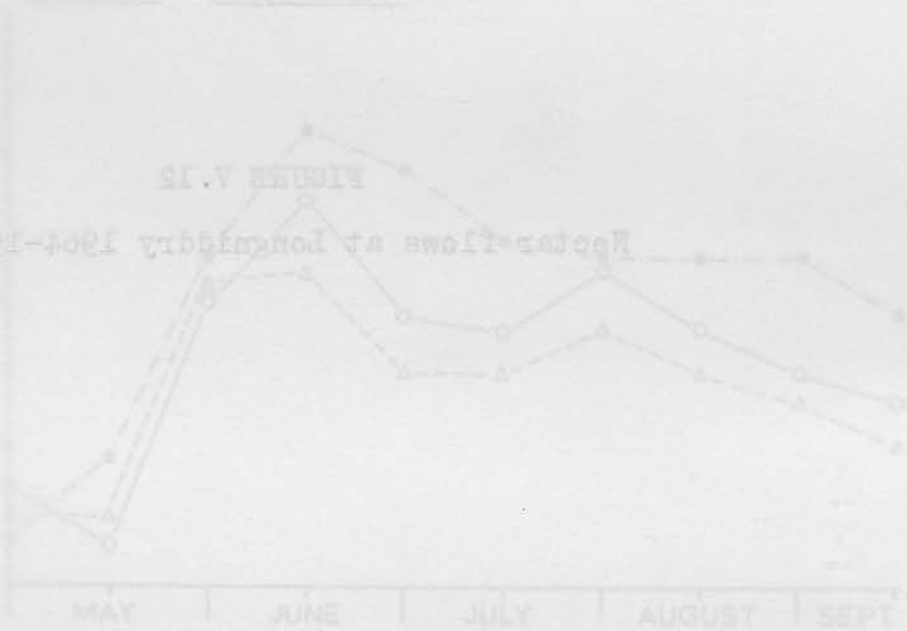

MAY
JUNE
JULY
AUGUST
SEPT

FIGURE V.12

Nectar flows at Longniddry 1964-1966

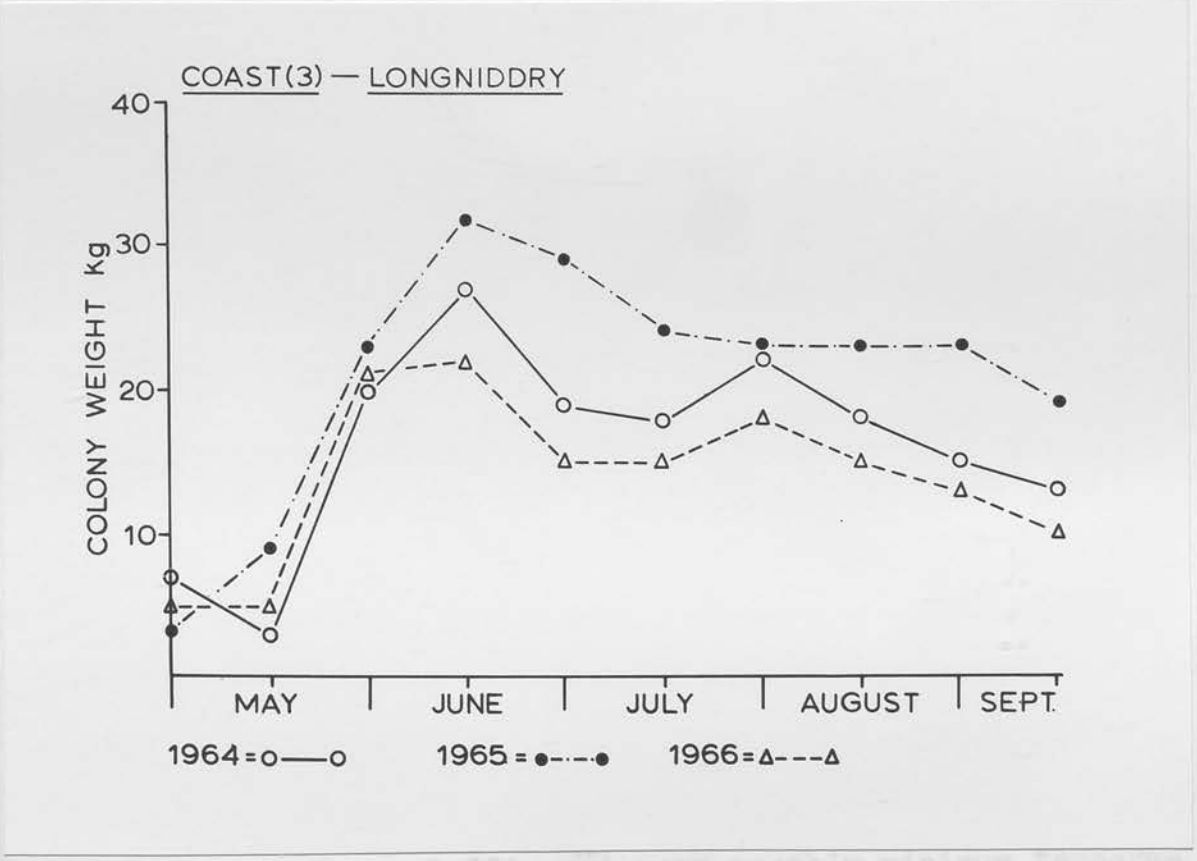

COAST(3) — LONGNIDDRY
COLONY WEIGHT Kg
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT.
1964 = o—o
1965 = ●-·-●
1966 = Δ- - -Δ

TABLE V.34

Mean colony weights (kg) for 3 years on upland and coastal sites

Date	30 April	15 May	30 May	15 June	30 June	15 July	30 July	15 Aug.	30 Aug.	15 Sept.
Coastal sites	4.1 kg	4.6	17.1	23.0	18.0	14.7	11.4	15.2	13.5	10.6
Upland sites	5.6	2.6	12.3	14.4	13.8	17.5	26.0	31.2	38.5	36.1
Significance between them	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	*

Weather and nectar flows

The relationship between weather conditions and the occurrence of nectar flows was examined using the 'Monthly Weather Report' (Anon, 1964-6) of the Meteorological Office and the data from the Bush apiary because of its proximity to a weather station. The correlation coefficient of the rainfall (Table V.35,b), against colony weight change per month (Table V.35,a) from May to August during 1964 to 1966, $r = -0.16$, was not significant). Similarly, the correlation coefficients for, sunshine,per day per month (Table V.35,c) against colony hive weight change, $r = 0.05$, mean monthly maximum temperature (Table V.35,d) against colony hive weight change, $r = -0.003$, and mean monthly minimum temperature (Table V.35,d) against colony hive weight change, $r = -0.059$, were all found to be not significant. Thus there were no significant correlations between rainfall, sunshine and temperature on the one hand and the weight change

of colonies of honeybees at Bush on the other. It should be noted however that in 1965 the very wet July coincided with a poor honey harvest, and that on the coastal sites in 1964 there was good weather present while at the same time no nectar was being harvested (Table 8.2 of Appendix 8).

TABLE V.35

The relationship between weather and colony weight gain (kg) at Bush 1964, 1965 and 1966

(a) Colony weight change (kg)

Year	May	June	July	August
1964	+ 14 kg	+ 7	+ 10	+ 20
1965	+ 14	- 6	- 6	+ 13
1966	+ 7	- 1	+ 8	+ 14

(b) Rainfall per month[1] (mm)

1964	51 mm	60	31	76
1965	72	73	142	77
1966	48	118	55	198

(c) Average daily sunshine per day per month[1] (hours)

1964	4.99 h	6.29	5.40	4.58
1965	4.45	5.58	3.68	5.55
1966	6.97	3.55	6.17	3.23

(d) Mean monthly temperatures, maximum and minimum[1] (°C)

1964	13.7-6.7°C	15.5-8.2	17.0-9.8	16.6-9.3
1965	13.2-5.4	16.2-8.8	14.5-7.7	16.5-8.4
1966	14.4-4.7	16.1-9.3	17.1-8.9	16.1-9.3

[1]Climatic data abstracted from the 'Monthly Weather Report' (Anon, 1964-6).

V.6 Chemical composition of pollens

Dry matter

Over 250 samples of pollen gathered from 4 different sites throughout the 1969 season had a mean dry matter and standard error of 73.3 $\pm$ 0.3%. This value did not vary very greatly from site to site nor throughout the season (Table V.36). In September the Bush pollen moisture was fairly high and the bees collected no pollen at Broadwood. The August data exhibited a greater variation than in any other month except September. When analyses of variance were performed to examine variations in dry matter between sites and between months, the August and September results were not included because of the large variation between their means. These analyses of variance indicated no significant difference ($p = 0.05$) between months for the pollen dry matters during May, June and July but a significant difference ($p = 0.05$) between the collections at Maggie's Waas Wood compared with those at the other sites.

Ether extract

Only beech and cruciferous pollens contained more than 4% of lipid material. Beech pollen contained significantly most ($p = 0.05$) lipid and cruciferous pollen contained significantly more lipid than any of the other pollens. This was not unexpected because under microscopic examination the beech pollen grains were found to contain large 'fatty' globules. The cruciferous pollen pellet grains

TABLE V.36

Mean % dry matter and its standard error for pollen harvested in 1969

Site	May	June	July	August	September
Penicuik	74.4±2.04(4)	73.4±0.57(20)	75.3±0.95(16)	72.8±1.91(12)	71.5±4.03(6)
Bush	74.2±1.02(8)	74.7±0.56(24)	76.0±0.55(16)	70.6±1.29(13)	63.9±1.34(8)
Broadwood	75.0±2.10(4)	73.2±0.92(24)	74.8±0.85(20)	76.1±1.08(15)	No Pollen collected by bees
Maggie's Waas	72.4±1.44(7)	72.3±0.60(24)	71.5±1.73(16)	72.7±1.39(12)	71.8±2.38(4)

(Numbers of observations in each mean are included in parenthesis)

were difficult to separate from each other without using a suitable organic solvent (ethanol) to dissolve away the outside coat of lipid material (Table V.37).

TABLE V.37

The ether extract of pollens (as % dry matter)

Pollen type	Ether extract means	S.E. of difference between ether extract means
Beech	11.8	
Buttercups	2.3	
Crucifers	7.8	± 0.92
Heaths	1.7	
Rosebay willow-herb	2.0	
Sycamore	3.6	
White clover	2.7	
General mean	4.6	

Nitrogen

The mean nitrogen contents of 7 main pollen types are given in Table V.38. Each mean nitrogen value represents the mean of 7 separate samples.

TABLE V.38

Mean Nitrogen values of pollens (as % dry matter)

Pollen type	Nitrogen	S.E. of difference between means	Crude Protein value (N x 6.25)
Sycamore	5.56		34.8
Crucifers	4.91		30.7
White clover	4.68		29.3
Heaths	3.52	± 0.19	22.0
Rosebay willow-herb	3.52		22.0
Buttercups	3.10		19.4
Beech	2.58		16.1
General mean	3.98		24.9

An analysis of variance indicated that significant differences ($p = 0.05$) existed between the nitrogen contents of the pollens examined except between those of crucifers and white clover on the one hand and heaths and rosebay willow-herb on the other. Sycamore pollen contained the highest amount of nitrogen and beech tree pollen the least.

Carbohydrates and other compounds

The results of these analyses are given in Tables V.39, 40 and 41. The mean total sugar content (Table V.39) was about one third (31%) of the dry matter of the pollens (range 22.4% - crucifers, to 42.4% - heaths); fructose with a general mean of 19.0% made up the largest part of this (range 14.2% - sycamore to 24.8% - heaths), with glucose, general mean 9.9%, being the largest part of the

remainder (range 3.5% - crucifers, to 17.2% - heaths). Heath pollen had a consistently high total sugar content; in all analyses both the fructose and glucose contents were higher than in any other pollen but fructose was consistently present in greater amounts. In all cases the glucose content of the pollen was lower than that of the fructose although the ratio of these two sugars fluctuated from about 1:1 to 1:3. The 'lignin' fraction of the pollens (Table V.40) which consisted of 72% sulphuric acid insoluble organic material was quite considerable, representing 16.2% of the mean pollen dry matter (range, 10.8% - heaths, to 22.2% - crucifers). A further examination of these pollens (Table V.39) indicated that the 'hemicelluloses' which were extracted in the N sulphuric acid treatment and were thought to consist mostly of 'xylan' (Shaw and Yeadon, 1966) had a general mean of 7.2% of the pollen dry matter (range 4.0% - sycamore, to 15.2% - buttercups). The xylan content of buttercups was significantly higher than any of the other pollens. 'Cellulose' which was the extract from the treatment with 72% sulphuric acid was a very small constituent of pollen, general mean 0.52% dry matter, and starch was not detected in these pollens at all. The general mean value of the undetermined matter of these pollens (Table V.41) was 12.3% dry matter and was highest in beech (24.3%) and lowest in crucifers (8.5%); it is probable that at least part of this 'undetermined matter' was pollenin (Lunden, 1954) which consists mostly of a mixture of simple dicarboxylic acids (Shaw and Yeaden, 1964).

TABLE V.39

Analysis of pollen carbohydrates (as % dry matter; means of 4 samples - Appendix 10)

Pollen types	Glucose	Fructose	Total sugar	'Xylan'	'Cellulose'
Beech	6.0	17.1	26.8	3.5	0.26
Buttercups	15.9	18.6	35.7	15.2	0.74
Crucifers	3.5	16.6	22.4	3.8	0.76
Heaths	17.2	24.8	42.4	9.5	0.18
Rosebay willow-herb	8.5	20.6	36.3	9.5	0.64
Sycamore	11.8	14.2	27.1	4.0	0.60
White clover	6.5	21.2	28.5	5.0	0.48
General mean	9.9	19.0	31.3	7.2	0.52
S.E. of difference between means	± 0.40	± 1.04	± 3.81	± 0.23	± 0.10

TABLE V.40

The % ash and 'lignin' in pollen (as % dry matter; means of 4 samples - Appendix 10)

Pollen types	Ash means	'Lignin' means
Beech	1.95	15.3
Buttercups	2.85	14.9
Crucifers	3.84	22.2
Heaths	2.76	10.8
Rosebay willow-herb	2.81	15.2
Sycamore	3.39	14.7
White clover	3.29	20.4
General mean	2.98	16.2
S.E. of difference between means	± 0.166	± 0.18

TABLE V.41

Pollen undetermined matter (by subtraction)

Pollen type	Mean % undetermined matter
Beech	24.3
Buttercups	8.9
Crucifers	8.5
Heaths	10.7
Rosebay willow-herb	11.6
Sycamore	11.8
White clover	10.3
General mean	12.3

Ash and minerals

About 3% of the pollen was ash (Table V.40) and about half of this was calcium, magnesium, manganese, phosphorus, potassium and sodium; the mean concentrations are described in Table V.42).

TABLE V.42

The mean mineral content of pollen

Pollen type	Ca	Mg	K	Na	Mn	P
Beech	0.047	0.084	0.97	0.013	23	0.35
Buttercups	0.081	0.140	1.21	0.035	42	0.48
Crucifers	0.189	0.146	1.34	0.035	17	0.51
Heaths	0.176	0.079	0.93	0.017	209	0.34
Sycamore	0.093	0.112	1.16	0.021	53	0.51
White clover	0.167	0.089	0.81	0.011	21	0.18
Rosebay willow-herb	0.122	0.098	1.04	0.013	14	0.34
Means	0.125	0.107	1.066	0.021	54	0.39
S.E.	± 0.0264	± 0.006			± 2.4	
significance	**	**	n.s.	n.s.	**	n.s.

(Mn values are parts per million dry matter, all others are % dry matter. Standard errors are those of the differences between the pollen means).

Analyses of variance were performed on the values of these elements found in the pollen. These analyses indicated

that only the calcium, magnesium and manganese contents of some pollens were significantly different from others. Heath pollens had much higher manganese contents than the other pollens, and rosebay willow-herb had the lowest; cruciferous pollens contained the highest calcium and beech the lowest; cruciferous pollens also had the highest magnesium content and heaths had the lowest. The mean phosphorus content of the pollen was 0.39% of the dry matter.

Gross energy

The mean gross energy of 3 different samples of mixed pollen was 5458 ± 165 calories per gram (Table V.43) after correcting for nitrogen and sulphur.

TABLE V.43
Gross energy values of pollen

sample	
1	5310 Calories per g. dry matter
2	5275
3	5789
Mean and s.e.	5458 ± 165

(Correction for nitrogen and sulphur 19 cal/g.)

Nucleic acids

No values higher than 0.5% of the dry matter were found, when crucifers, heaths, white clover, rosebay willow-herb, sycamore, buttercups and beech pollens were examined.

Amino acids

The amino acid contents of the 7 pollen types examined are described in Table V.44, where they are presented as percentages of the crude protein. From 39 to 43% of the crude protein values were accounted for by the 9 essential amino acids (Groot, 1953) examined. Between 80 and 87% of the crude protein consisted of the amino acids determined here.

An analysis of variance of the amounts of the different amino acids found in the pollens indicated that, of the 16 determined, only 3, serine, cystine and histidine were present in amounts that were significantly different ($p = 0.05$) from each other. Buttercup pollen had a significantly higher ($p = 0.05$) amount of serine than crucifer, beech, heath and sycamore or white clover pollen but not willow herb, while willow herb pollen was significantly higher ($p = 0.05$) in serine than heath, beech, sycamore and white clover. Crucifer pollen was significantly higher ($p = 0.05$) in cystine than all the other pollens except that of buttercup while willow herb pollen was significantly lower ($p = 0.05$) in cystine and significantly higher in histidine than the other pollens.

The results of the amino acid analysis of the worker honeybees are presented in Table V.45. An analysis of variance indicated that the differences in the relative amounts of the various amino acids in the different adult worker honeybees were very small, except in the cases of glycine, alanine and lysine.

TABLE V.44

The amino acid analysis of pollens (g/16gN)

Pollen amino acid	Beech	Buttercups	Crucifers	Heaths	Sycamore	White clover	Rosebay willow-herb	Standard error between pollen means	Significance	General means
Aspartic acid	10.00	10.16	9.54	9.74	10.29	9.98	9.95	0.747	n.s.	9.96
Threonine	4.83	5.51	4.91	4.63	4.63	4.48	4.94	0.344	n.s.	4.84
Serine[1]	5.06[a]	6.11[b]	5.49[ac]	5.23[a]	5.01[a]	5.05[a]	6.05[bc]	0.244	*	5.43
Glutamic acid	12.33	11.85	11.20	10.94	11.69	11.87	10.80	1.301	n.s.	11.52
Glycine	5.17	5.22	4.95	4.83	5.16	4.49	4.46	0.592	n.s.	4.89
Alanine	5.60	4.91	5.09	5.20	5.40	5.23	5.60	0.597	n.s.	5.21
Valine	6.03	5.65	4.87	5.39	5.74	5.25	5.24	0.571	n.s.	5.45
Cystine[1]	1.35[bcd]	1.61[b]	2.04[a]	1.48[bc]	1.22[cde]	1.19[cde]	0.71[f]	0.111	*	1.37
Methionine	2.02	2.64	2.13	1.87	2.14	2.19	2.34	0.253	n.s.	2.19
Isoleucine	4.76	4.89	4.37	4.45	4.96	4.51	4.31	0.642	n.s.	4.61
Leucine	7.01	4.50	6.61	7.06	7.22	7.00	7.26	0.713	n.s.	7.09
Tyrosine	3.41	3.78	2.98	3.27	3.69	3.48	3.52	0.359	n.s.	3.44
Phenylalanine	5.09	4.72	4.10	4.35	4.71	4.51	4.43	0.650	n.s.	4.56
Lysine	5.66	5.76	6.12	4.58	3.69	4.69	5.85	1.090	n.s.	5.19
Histidine[1]	2.03[a]	1.87[a]	1.92[a]	1.97[a]	1.76[a]	1.99[a]	3.59[b]	0.310	*	2.16
Arginine	5.66	4.98	4.67	5.90	4.16	4.74	5.16	0.529	n.s.	5.04
Total recovered	85.44	87.13	80.98	80.85	81.44	80.62	84.23	6.401	n.s.	82.95

[1]Within row means with one or more common letters included in the superscript are not significantly different (p = 0.05) as assessed by Duncan's multiple range test.

TABLE V.45

The amino acid analysis of honeybees, Apis mellifera L., (g/16gN)

Honeybee[1] / Amino acid	A	B	C	D	Standard error of difference between honeybee means	Significance	General means
Aspartic acid	7.29	7.40	6.56	7.43	0.471	n.s.	7.17
Threonine	3.64	3.49	3.55	3.72	0.096	n.s.	3.60
Serine	4.47	4.26	4.15	4.25	0.125	n.s.	4.28
Glutamic acid	10.66	10.13	10.80	9.96	0.746	n.s.	10.39
Glycine[2]	7.97[a]	6.98[b]	7.22[b]	7.21[b]	0.136	*	7.35
Alanine[2]	8.56[a]	7.22[b]	6.87[b]	7.74[ab]	0.325	*	7.60
Valine	6.19	5.68	5.74	6.10	0.172	n.s.	5.93
Cystine	0.96	5.20	1.14	1.05	3.130	n.s.	2.09
Methionine	1.32	1.24	1.30	1.39	0.043	n.s.	1.31
Isoleucine	4.75	4.47	4.69	4.87	0.172	n.s.	4.70
Leucine	7.63	7.10	7.41	7.99	0.195	n.s.	7.53
Tyrosine	3.85	3.43	4.08	3.72	0.430	n.s.	3.77
Phenylalanine	3.02	3.05	3.42	3.22	0.212	n.s.	3.18
Lysine[2]	4.79[ab]	4.67[b]	4.90[a]	3.87[c]	0.063	*	4.56
Histidine	2.35	2.18	2.35	2.17	0.150	n.s.	2.26
Arginine	4.08	4.31	4.09	4.32	0.381	n.s.	4.20
Total recovered	81.53	76.51	78.27	79.02	1.208	n.s.	78.83

[1] see chemical analyses in experimental

[2] Within row means with one or more common letters included in the superscript are not significantly different (p = 0.05) as assessed by Duncan's multiple range test.

V.7 Honey

Honey cations

The results of the analyses of the honey samples are presented in Table V.46 and the distributions are depicted in Figures V.13 - 16.

TABLE V.46

The sodium, potassium, calcium and magnesium content of honey

Element	No. of samples	Means[1]	Range[1]	D.M. means[2]	Pollen means[3]
Na	97	75	25 - 178	92	210
K	97	1480	133 - 4680	1805	10,660
Ca	93	151	30 - 530	184	1,250
Mg	90	90	8 - 160	110	1,070

[1]Ppm wt/vol.

[2]Assuming 18% moisture in honey.

[3]See Table V.42

In 87 samples of honey all 4 cations were determined. These quantities were converted into milli-equivalent weights/volume and used to investigate the relationship between the ions by calculating the total, partial and multiple correlation coefficients (Table V.47).

FIGURE V.13

The calcium content of honey

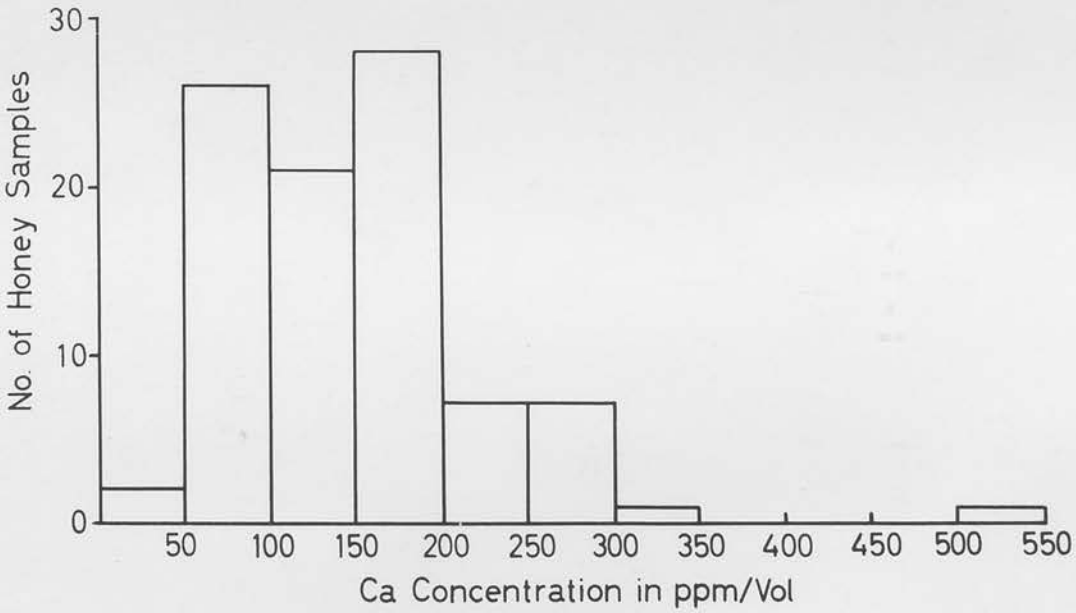

30
20
10
0
No. of Honey Samples
50
100
150
200
250
300
350
400
450
500
550
Ca Concentration in ppm/Vol

FIGURE V.14

The magnesium content of honey

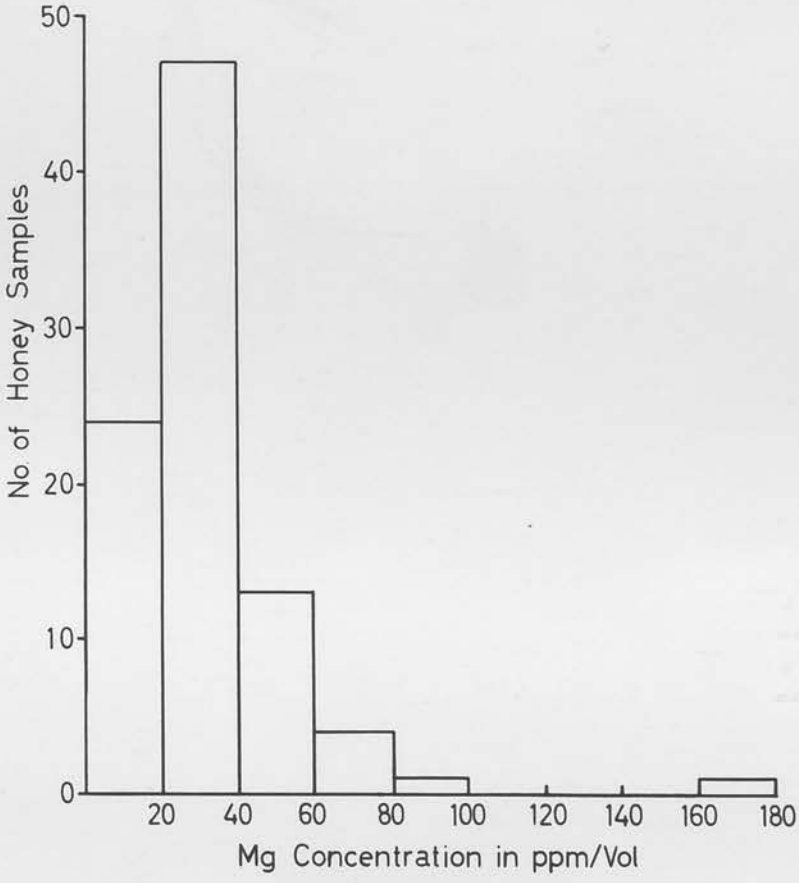
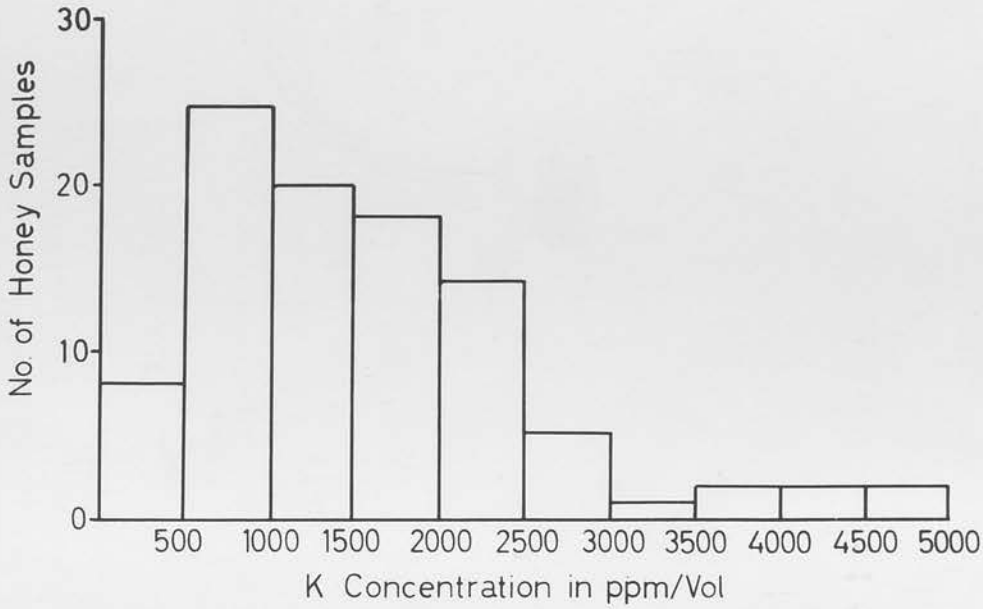

50
40
30
20
10
0
No. of Honey Samples
20
40
60
80
100
120
140
160
180
Mg Concentration in ppm/Vol

FIGURE V.15

The potassium content of honey


30
20
10
0
No. of Honey Samples
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
K Concentration in ppm/Vol

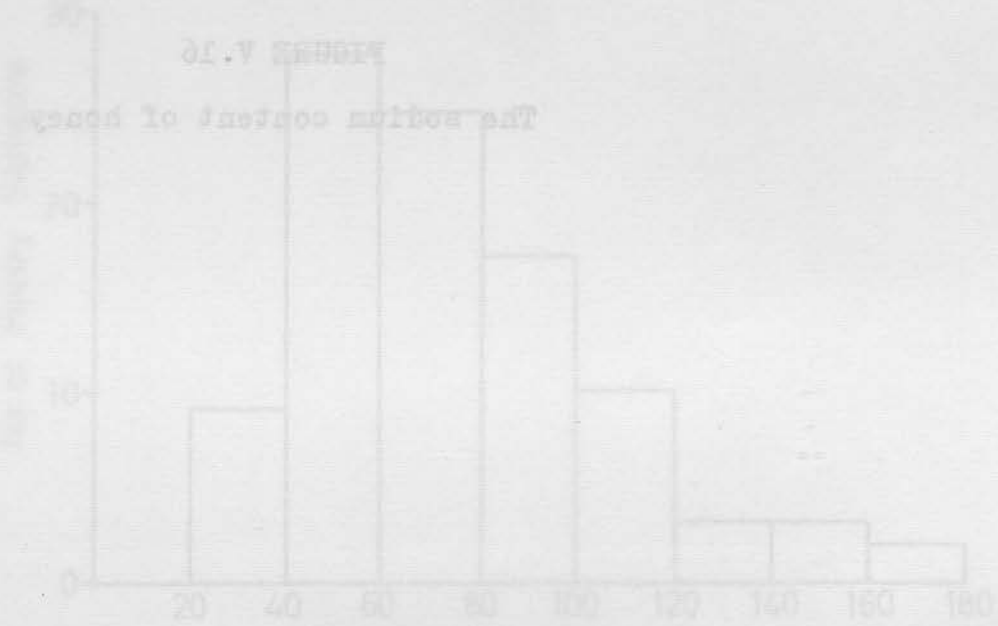

0
10
20
20
40
60
80
100
120
140
160
180
Na Concentration in ppm/Vol

FIGURE V.16

The sodium content of honey

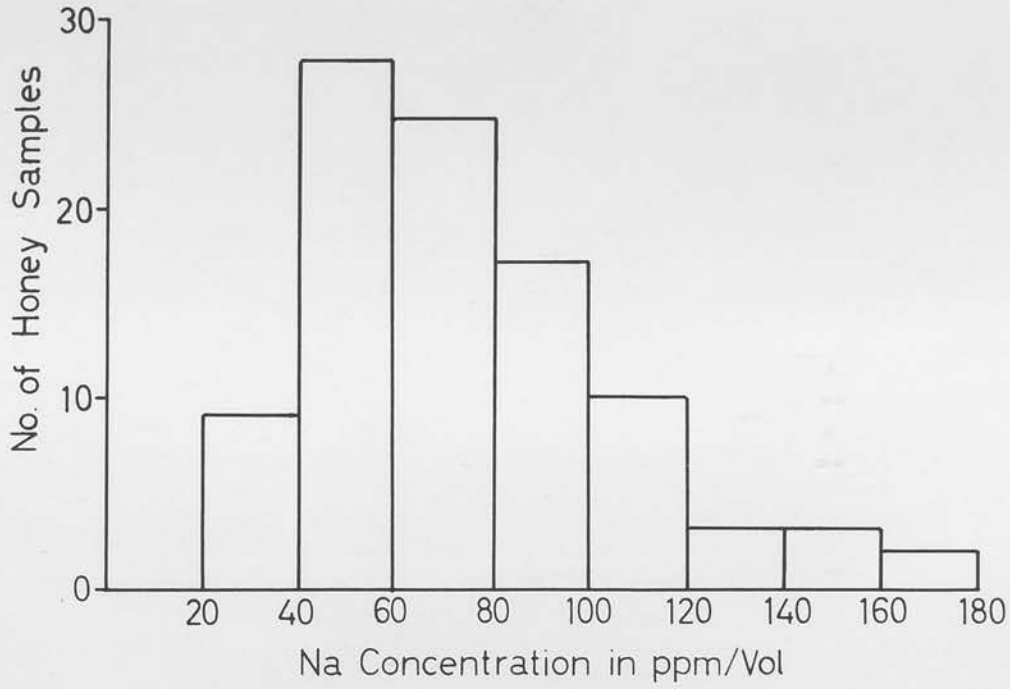

30
20
10
0
No. of Honey Samples
20
40
60
80
100
120
140
160
180
Na Concentration in ppm/Vol

TABLE V.47

The correlations between the Na, K, Ca and Mg content of 87 samples of honey (where 1 = Na, 2 = K, 3 = Ca and 4 = Mg in the correlation coefficients)

A. Total correlation coefficients for 2 variables.

$R_{12} = 0.320^{**}$; $R_{13} = 0.284^{**}$; $R_{14} = 0.181$;
$R_{23} = 0.357^{***}$; $R_{24} = 0.620^{***}$; $R_{34} = 0.382^{***}$

B. Partial correlation coefficients for 3 variables.

$R_{12.3} = 0.245^{*}$; $R_{12.4} = 0.270^{*}$; $R_{13.2} = 0.191$; $R_{13.4} = 0.236^{*}$;
$R_{14.2} = -0.024$; $R_{14.3} = 0.082$; $R_{23.1} = 0.293^{**}$; $R_{23.4} = 0.166$;
$R_{24.1} = 0.603^{***}$; $R_{24.3} = 0.560^{***}$; $R_{34.1} = 0.350^{**}$; $R_{34.2} = 0.219^{*}$

C. Partial correlations for 4 variables.

$R_{12.34} = 0.241^{*}$; $R_{13.24} = 0.202$; $R_{14.23} = -0.068$;
$R_{23.14} = 0.109$; $R_{24.13} = 0.559^{***}$; $R_{34.12} = 0.228^{*}$

D. Multiple correlation coefficients.

$R_{1.234} = 0.374^{***}$; $R_{2.134} = 0.660^{***}$; $R_{3.124} = 0.450^{***}$;
$R_{4.123} = 0.645^{***}$

These correlations indicated that, of the ion pairs, K and Mg were the most closely related and Na and Ca and Mg and K were the least; these relationships were not greatly affected by the relative amounts of the other cations present. The sodium / Mg concentrations were the most affected by the other ions and the ~~magnesium~~ / Ca ions were the least.

VI DISCUSSION

VI.1 Pollen gathering

The amount of pollen trapped and the total colony harvest of pollen

From 1963 to 1965 a mean weight of about 1 kg of pollen (1.068 ± 0.167, range 0.734 -1.729 kg fresh weight) per colony was harvested from the pollen traps at Bush. In 1969 when pollen trapping of honeybees was examined further with 16 colonies on 4 separate sites the mean amount of pollen harvested per colony was nearly 3 kg (2.989 ± 0.617, range 1.682 - 6.821 kg fresh weight). The greater amounts of pollen trapped in 1969 were due to the use of larger colonies compared with in the previous years (Section IV.4). The quantities of pollen trapped from colonies by Synge (1947) in the U.K. (1.4 - 1.5 kg), Hirschfelder (1951) in Germany (2.3 - 9.1 kg), and Louveaux (1958) in France (2.3 - 3.3 kg) are in closer agreement with the present results than those from the United States of America. For example, Todd and Bishop (1940) harvested 8 to 18 kg per colony and Eckert (1942) estimated that between 50 and 55 kg were gathered by a normal colony in a season. These larger pollen harvests in America were due in some instances to a relatively longer season (Todd and Bishop, 1940) and in others to the continued rotation of pollen traps from colony to colony (Eckert, 1942). Length of season, methods of trapping and colony size all appear to affect the amount

of pollen trapped but in the areas of Central and North-Western Europe studied, seasonal pollen harvests from pollen traps vary between 1 and 9 kg with mean values for medium to large colonies of from 2 to 3 kg; the amounts of pollen trapped in the South-East of Scotland fit into this general pattern.

The variation in the amount of pollen trapped within sites was much greater than between sites (Table V.2) and was thus mostly due to differences between colonies rather than between sites. This suggests that the availability of pollen from sites in this area was not a limiting factor for colony development during the period of experimentation although lack of availability had been noted at Bush for short periods in spring in other seasons before pollen harvesting had begun. Despite the fact that the amount of pollen collected by a colony is ultimately required to meet the demands of brood rearing for protein, only at the end of the season was a significant correlation found between the pollen trapped by the colonies and the brood reared (Table V.32). This lack of significance was probably due to colonies being out of phase with each other in their individual pollen collecting and perhaps also to the irregular intervals between observations because the correlation between the mean brood and the mean pollen trapped per day by the colonies, throughout the season was significant (Results V.4). This is in agreement with Free (1967) who claimed that increasing the amount of brood being reared

caused an increase in the amount of pollen collected. Pollen availability does not therefore appear to restrict brood rearing in this area.

An examination of the brood during 1969 showed that a mean number of 77,800 ($\pm$ 7,700) was reared by a colony between late May and mid-September (Appendix 2). For the same period of the active season, calculations based upon other observations (Allen and Jeffree, 1956) indicated that about 79,600 bees were reared. Furthermore if one accepts the estimate of 1 g of dry pollen being required to rear 10 worker honeybees (Todd and Bishop, 1940) then about 8 kg of dry pollen (3.2% N) would be required to rear the 80,000 honeybees which were produced by these colonies between late May and mid-September. This means that the colonies fitted with pollen traps were gathering over the season 27.5% more pollen than was required to rear the total amount of brood produced during this period and that this pollen amounted to about 3 kg (2.2 kg dry matter). That is 22% of the total pollen harvested was trapped which compares favourably with Synge's estimate of 25% of the pollen entering the colony being removed by the trap. In fact the estimate of 8 kg of pollen (dry matter) being required by a colony of honeybees for brood rearing over the active pollen collecting season is fairly close to the estimate of 5.6 to 5.9 kg (Synge, 1947) and 8 to 11 kg (Todd and Bishop, 1940; adjusted for 80,000 bees) the exact amount varying with the protein content of the pollens. These figures are however much

smaller than the comparable estimates made by Hirschfelder (1951), 17 to 27 kg; and Louveaux (1958), 23 to 33 kg, from trapping returns. It is often impossible to be certain exactly what investigators mean when they refer to pollen because they often do not state whether it is fresh, air dry or oven dry pollen to which they are referring. When the amount of pollen required to rear the brood was calculated using the relationship described by Todd and Bishop (1940) and noted above, the pollen trapped did not bear a fixed relationship to the estimate of the total pollen harvest based upon the amount of brood reared but fluctuated continuously throughout the whole period, (Appendix 2, Table 2.2) with a colony mean seasonal range between 6 and 92 percent of the requirement. The largest and the smallest relative amounts of pollen were trapped at the maximum brood rearing time in mid-summer and at the end of the season when brood rearing had virtually ceased indicating that congestion of pollen foragers at the colony entrance might be an important factor affecting the amount of the pollen harvest actually trapped. One should also bear in mind that these calculated figures for the percentage of pollen harvested may be open to at least one source of error because of the 'buffering effect' of the protein reserves in nurse bees (Discussion Vi.4). Synge (1947), Louveaux (1958) and Free (1967) have all stated that pollen traps cull a certain fixed percentage of the total pollen harvest continually from all the colonies throughout the pollen collecting season and Hirschfelder

(1951) has claimed that different colonies have different but fixed amounts of the total pollen harvest culled off by traps (range 15 to 43%). The present study using a different method of approaching the problem indicates that the percentage of the total pollen harvest collected by the traps appears to vary continuously throughout the season, relatively more being lost to the trap when congestion at the colony entrance is most intense. More attention should be paid to this than has been the case in the past.

The period of pollen collection

The period when honeybees collect pollen in quantity is of great interest because it defines the length of the active season for this insect. At Bush between 1963 and 1965 this active season was on average 121 days in length and did not vary greatly in different years, and in 1969 the mean length of the pollen collecting period on the different sites was 107 days. Pollen traps operating from the beginning of the year indicated that this active season began on the same day for all colonies on the same site and in 1969 when several sites over a wide area were examined it also occurred on the same day on all sites. Pollen foraging by colonies ceased in a much less regular manner which appeared to be affected more by colony individuality than the environment; in 1969 when this feature was examined more closely, not only were wide variations between colonies on the same site observed, but also the coastal colonies finished collecting pollen earlier than those inland although

this feature was found to be significant for only one coastal site compared with the inland ones (Table V.6). This difference between sites appeared to be related to the occurence of nectar flows because the latter appeared to stimulate brood rearing (Table V.29).

It is difficult to compare these observations with those from other countries because of the different conditions and the few records available, but Synge (1947) in the South of England and Louveaux (1958, 1959) in France appear to have experienced pollen collecting seasons of about 200 and 210 days respectively. These variations are perhaps mainly due to the temperature dependent nature of the flowering process and consequently the further south one travels in Europe the longer the pollen season will tend to become. The mean monthly shade temperature at Bush from 1963 to 1965 (Table V.35) between November and March was continually below 10°C, the temperature below which honeybee flight virtually ceases (Bodenheimer and Ben Nerya, 1937). Thus it is not surprising thatlittle or no pollen was gathered at Bush between November and April to May. Furthermore pollen collecting by honeybees occurred when protein was required to sustain the major period of brood rearing. Thus the honeybee, like most animals, rears most of its young when the appropriate food supplies are most abundant.

The pollen harvesting rate

The amount of pollen trapped daily by colonies of honeybees fluctuated considerably (Table 3.4; colony H,1964)

probably mainly due to the interplay of climatic and floral factors. These phenomena have been discussed by Percival (1947) and Synge (1947). When the general implications of the pollen income of honeybee colonies are being considered it is perhaps better to examine general trends rather than daily fluctuations. Between 1963 and 1965 much more pollen was harvested in the first half of the season than in the second (Table V.5); this reflected a higher demand occurring earlier in the season presumably for brood rearing which is at its peak about mid-summer (Figure V.3).

In 1969 a more detailed analysis of this situation was possible and this indicated that the amount of pollen collected rose rapidly to a maximum of 124 g per day in early June and then declined each month until none was gathered in October. This pattern was similar on all the sites, showing that site differences did not have much influence on this tendency which appeared to be a consequence of the brood rearing requirements of the colonies. Few records from comparable temperate areas are available, but in Germany (Hirschfelder, 1951) and France (Louveaux, 1958) the pollen harvest began earlier in the year and increased less rapidly to a maximum in June before declining. Thus the more northerly latitude of Scotland did not alter the time of year when maximal pollen harvesting occurred although it did shorten the period between the onset of pollen gathering and the maximum. When some other trapping records were examined (Todd and Bishop, 1940; Rashad and Parker, 1958a, 1958b),

they appeared to be influenced by the availability of pollen, which in the tropics and sub-tropics is affected by the rainy season (Smith, 1960) and as a consequence, the brood cycle of colonies in such areas is often divided into two parts (Bodenheimer and Ben Nerya, 1937). In northern Europe where the production of pollen by plants is generally restricted to the summer season pollen is harvested by honeybees to a pattern of demand which is influenced by colony requirements for brood rearing (Free, 1967). In the present study and that of Allen (1965a) the regular increase in brood rearing to a maximum in mid-summer and then a gradual decrease as winter approached (Figure V.3) appeared to indicate that pollen supplies were abundant and did not restrict the natural development of the brood rearing cycle as in the tropics and sub-tropics (Bodenheimer and Ben Nerya, 1937).

Honey and pollen harvests

There was an inverse relationship between the amounts of pollen trapped from colonies in 1963 to 1965 and the quantity of honey stored as indicated by a weighed colony. A rather similar observation had been made by Ribbands (1949) when he noted that honeybees preferred nectar to pollen crops. Louveaux (1958, 1959) however thought that there was no clear correlation between the harvesting of pollen and nectar, and indeed the analysis of the 1969 data from the present study indicated that pollen harvesting was unrelated to the amount of honey stored except perhaps in

September. Even then the correlation found might be significant only because larger colonies appeared to store more honey and rear more brood in the autumn and consequently might gather more pollen to feed this brood.

The number of pollen types gathered by colonies of honeybees each season

In the early study at Bush between 1963 and 1965 it was observed that very few flowers were used for pollen production by honeybees at a particular site. The mean number of pollens gathered by a colony over this period was 13 (range 10 - 17). In fact there was a tendency for the honeybees to harvest only the same few main pollens from the Bush area season after season, indicating that the important pollen producing species of an area could be characterised by pollen traps in one season provided the flora remained undisturbed.

In 1969 an extension of these observations on the number of pollen types gathered by colonies of honeybees each season to 3 other sites besides Bush showed that this was a more general phenomenon because the mean numbers of pollen types harvested per colony remained low at 15. Also an analysis of variance showed that the variability between the numbers of pollens gathered by different colonies was greater than the differences in numbers of pollens gathered between sites. In the areas examined, which were fairly representative of the South-East of Scotland, the numbers of species of pollen harvested between sites and in different seasons on the same site appeared to be fairly similar.

Other workers, for example, Andrewjew (1928) in Russia, Synge (1947) in the South of England, Percival (1947) in South Wales, Louveaux (1958, 1959) in France have all reported more species in their pollen collections. These differences were not very great and are probably due in part at least to a richer flora, because, apart from local variations, floras generally tend to suffer a general reduction in species as one travels further north.

The relative amounts of different pollen types trapped from honeybees

Very few pollen types dominated the pollen harvest at Bush between 1963 and 1965 and that from Bush and the other sites in 1969 (Table VI.1).

TABLE VI.1

Total number of pollens types trapped altogether, and in amounts less than 1% of these collections

Sites	Total No. of pollen types collected	No. of pollen types collected in amounts less than 1% of the total
Bush 1963-1965	22	12
All sites 1969	32	21

Similar patterns can be obtained from the observations made by Synge (1947), Percival (1947), Louveaux (1958) and others. This also indicates that comparisons between total and individual collections from sites or groups of sites can be examined by using the concept of diversity, a term used by ecologists to describe the relationship between

the number of species and number of individuals in a community and which is independent of population density or size. It was developed by Williams (1964) to characterise and compare collections of Lepidoptera caught in light traps. Indices of diversity (D) are calculated which show whether there are relatively few (low index) or many (high index) species in a collection (Appendix 5). Computation of this index can be simplifed using a normogram (Lewis and Taylor, 1966). The indices of diversity for the pollen collections at Bush between 1963 and 1965 were low, varying from 1 to 3, and similar results were found for the 1969 harvests indicating that there was no great diversity between the different pollen collections either in the different years at Bush or the different sites in 1969. Calculation of these indices for the data presented by Synge (1947) and Percival (1947) produced a value of $D = 4 \pm 0.6$. Thus the relationship of pollen types to pollen collections was very similar in both these pollen collections, a fact which is not immediately obvious from their original data. Furthermore there were more species in each of these harvests than in any of the present collections, probably because of the richer flora in the South of the U.K.

The number of different pollen types gathered each month

During the 1963-1965 period at Bush the monthly number of different pollen types harvested each year, although few compared with the total numbers of flowering plants available, increased to a maximum about mid-summer and then decreased;

a similar pattern was observed in 1969 when there was no significant difference between sites. One can also find evidence for this in the results presented by Percival (1947). One explanation for this could be that honeybees are essentially conservative insects, harvesting pollen from very few sources, but as the demands of brood rearing increase they are forced to utilise more floral types and when pollen demands decline the number of species from which pollen is harvested also declines. There is also the simple fact that more flowers are presenting pollen in some months than others so that there is a greater choice of pollens for the honeybees and this may be reflected in the numbers of different pollen types gathered each month.

Pollen preferences

Differences in the relative amounts of the same pollen types harvested by different colonies at Bush between 1963 and 1965, and within groups of colonies on different sites in 1969 indicates that colonies of honeybees appear to have preferences for particular pollens. These preferences could be partly inferred from the breeding of the "Lucerne bee" by Mackensen and Nye (1966, 1969), but the method of foraging used by honeybees may also be implicated. Apparently very few scout bees from a colony actually search for crops and nearly all the potential foragers await recruitment via the dancing of their successful colleagues (Oetingen-Spielberg, 1949). Thus if a colony discovers a source of pollen before another colony, then the method of

recruitment of foragers described above could produce variations in the relative amounts of these pollens harvested by the two colonies. In actual field conditions, probably inherited preferences and this method of recruitment are both involved.

The seasonal distribution of pollen sources

At Bush between 1963 and 1965 the pollen season usually began suddenly about the middle of May with sycamore as the most important source although this was occasionally displaced by beech. In early June cruciferous pollens from wild radish and charlock vied with white clover pollen as the main sources and remained so until the end of the pollen gathering season in early October. Occasionally in early June, raspberry was a fairly important source of pollen with buttercup more regular but less important in late June. In July rosebay willow-herb was fairly often gathered in large quantities by some colonies. During August and September, ericaceous pollens, mainly from bell and ling heathers, were common. Throughout the season most minor pollens were gathered in an erratic manner with the exception of those from composites which were often important subsidary sources especially during the first few weeks of the pollen season.

In 1969, there were few differences between the pattern described above which applied to the inland sites and that at the coast, showing that differences in altitude had little effect upon the phenological behaviour of these flowering plants. The flowering times were a few weeks later than

those in the South of Wales (Percival, 1947) and in the South of England (Synge, 1947), for example hawthorn was gathered between 3rd May and 25 th June in the East of Scotland in 1969 and between 28th April and 26th May in South Wales (Percival, 1947) and between 7th and 28th May in the South of England)Synge, 1947). Both these observations were made in late seasons. The differences in flowering times in the different parts of the U.K. have been examined by Jeffree (1958b) who stated that there was about a 3 week difference between Bristol and Aberdeen.

Land use and pollen collections

Most pollen collected at Bush between 1963 and 1965 was gathered from trees and plants associated with mixed woodland. One half of the remainder was collected from meadow and moorland plants and the other half from the weeds of arable ground. No pollen was gathered from coniferous trees. An examination of the area occupied by each of these habitats within 1000 metres of the colonies on each site, which was the area within which most of the foraging by these bees was likely to occur (Beutler, 1954), indicated that mixed woodland was the smallest, meadowland the largest, and arable land intermediate in the amount of ground they occupied. A calculation of the pollen harvested from a unit of area of each of these habitats showed that mixed woodland was much better than the others and that arable land was slightly better than meadowland.

In 1969 when 3 other sites besides Bush were examined, woodland pollens again predominated over those collected from meadow and arable land. Furthermore the relative amounts of pollen harvested from these different habitats on the 4 sites were shown to be significantly different from each other indicating consistent preferences by honeybees from different colonies at a given site for pollens associated with these particular habitats. The total pollen production per unit area of the different habitats on these sites also showed once again that much more pollen was collected from a unit of mixed woodland than from any other habitat and also that there was generally a lower collection rate and a greater variation in the amounts harvested from arable and meadowland.

A consideration of the plants involved in the pollen collections indicated that the relatively high production from mixed woodland was mostly due to the early flowering sycamore and beech trees and the importance of this habitat as a pollen producer decreased later in the season. The pollen harvested from arable areas was mainly from cruciferous weeds although poppy pollen was also collected on the coast. White clover was the most important pollen of meadow areas and the relatively large harvest from this plant on one site, Maggie's Waas, where there was very little meadowland indicated that the honeybees were flying slightly further than 1000 metres to forage for this pollen on the neighbouring golf course, perhaps because there were no other suitable sources of pollen at that time of year

(July). The relatively high production of pollen from mixed woodland trees and shrubs is perhaps not surprising when it is realised that honeybees are essentially insects that evolved in a woodland habitat. It is also important to bear this in mind when one is considering sites for colonies of honeybees. In fact one could perhaps imagine, after studying the present data, that in the future after some other investigations along similar lines have clarified the situation further, that using a suitable scale of map (1 to 10,560, that is 6" to 1 mile) and calculating the relative proportions of the four habitats of mixed woodland, meadow and moorland, arable land, and coniferous woodland within 1000 metres of any proposed site for colonies of honeybees one would be able to forecast the types and relative amounts of pollens that might be harvested by these bees if placed on that site especially if the habitats had been examined for the occurrence of those flowers whose pollens have been found to be harvested in relatively large quantities by honeybees. Changing methods of weed control may of course alter the pollens produced from arable land and in fact colonies of honeybees fitted with pollen traps could perhaps be used to monitor the efficiency of different methods of controlling cruciferous and papaverous weeds.

It is impossible to make direct comparisons of this data with that of any similar study because this aspect of pollen production does not appear to have been considered in any detail although an examination of pollen collections made elsewhere in Britain by Synge (1947) and Percival (1947)

appears to confirm the relative importance of mixed woodland and arable land as sources of pollen for honeybees.

VI.2 The effect of pollen traps on colonies of honeybees

Honey stored

Mid-June was the only time throughout the whole active season when there was significantly less honey in store in the trapped colonies. The large amounts of pollen being trapped in June showed that large numbers of the flying force were foraging for pollen. Pollen lost to the traps apparently caused a readjustment in the duties of the foraging force so that significantly smaller amounts of honey were then stored by the colonies being trapped (Table V.28). The rapidity with which this difference between trapped and untrapped colonies disappeared indicated how quickly the honeybees seemed to adapt to the restraint imposed by the traps and also emphasised how easily the effect of the trap on colonies could have been overlooked.

Several workers have claimed that pollen traps place much greater limitations on colonies of honeybees than indicated above. A closer inspection of their data showed that some of these claims were not completely justified. Hirschfelder (1951) for example stated that pollen traps reduced the honey production by about 20%, basing this claim on the simple difference between the amounts of honey gathered by the two groups. The harvest of pollen by traps over a 40 day period when a small quantity of nectar was

collected (Lavie and Fresnaye, 1963) was found to have little effect upon colony weights compared with controls. On another occasion Lavie (1967) claimed that pollen traps reduced the honey production of colonies by 24% but quoted no data that would have allowed a statistical test to verify this and so it is impossible to decide how meaningful these results really are.

Pollen stored

Only in early June was less pollen stored in the trapped compared with the untrapped colonies of honeybees. During the active season large amounts of pollen are required by all colonies to maintain brood rearing and a pollen store around the brood. A critical time for colonies occurs in early summer, when the demands for pollen to supply the exapanding brood nest are increasing. Apparently at this time the colonies whose pollen was being trapped were only able to harvest enough pollen to maintain brood production at a similar level to the untrapped colonies but were, for a short time, unable to store pollen at the same rate.

Adult honeybees

The only period during the active season when there was a significant reduction in the number of adult bees in the trapped colonies was noted between July and August. As no corresponding decline in brood rearing had occurred it appears that this phenomenon was a direct result of the traps injuring workers, as could be seen by the numbers of legs and wings which were found in the traps among the

pollen pellets, and so accelerating the rate at which the maximum adult population of these colonies declined. Traps did not however affect the population rate of growth, its maximum, or the number of bees entering the winter period (Table V.28).

Brood

The use of pollen traps did not have any significant effect on the amount of brood reared by honeybees at any-time during the active season. Although both Rybakov (1961) and Lavie (1967) support this view, the data they present cannot be examined statistically. Claims for the opposite viewpoint by Rashad and Parker (1958a) were also of doubtful value because a simple statistical examination of their results (a t-test) indicated that no significant effects of pollen traps on brood rearing could be detected.

Wintering

The colonies used for the 1969 experiment were inspected again in the spring of 1970 (Table V.31) when about 30% of the trapped and 13% of the untrapped colonies died. As normal winter losses expected are about 10% it appeared that the traps may have adversely affected the winter survival but this requires more investigation.

VI.3 Some effects of environmental variation on colonies of honeybees

In another section (VI.4) a study was made of the fluctuations in the honey stored; this reflected the nectar produced by coastal and inland sites throughout the active season (Table V.34). Significantly more honey was stored from the early flows by the coastal colonies and from the flows later in the season by those inland. In 1969 the effects of these variations in nectar availability on colonies of honeybees was examined. A greater storage of pollen was the only significant effect on colonies that experienced the better coastal nectar flows of spring. Perhaps nectar was being produced so easily that more foragers could be released for pollen harvesting, although actually no more pollen was trapped from the coastal colonies than compared with those inland. Towards the end of the season the relatively smaller amounts of pollen gathered and stored by coastal colonies reflected a reduction of brood rearing rather than a shortage of pollen if we agree with Free (1968) that brood rearing is the more fundamental phenomenon. There were no differences in the relative amounts of brood reared by the two groups of colonies until August when significantly more was produced by those inland which would reduce the relative age of this population. This stimulation of brood rearing can perhaps be attributed to the later nectar flows of the upland areas (Nolan, 1925). A significantly greater autumn adult population in the in-

land colonies was apparently caused by this late-season brood rearing but this increase in the adult population was not sustained probably due to a subsequently corresponding decrease in their numbers caused by the feeding of young (Maurizio, 1950). This late brood rearing of the inland colonies could be responsible for the fact that there was no increase in the amount of pollen stored although the pollen trapping rate was significantly elevated. There was no significant difference between the numbers of pollen types gathered on inland and coastal sites and, of the more important pollens only hawthorn was gathered on the coast in quantities that were significantly larger than those gathered at the inland sites.

The implications for practical beekeeping are as follows. In spring, honeybee colonies on the coastal sites stored more honey and pollen but this did not appear to have any significant lasting effect upon these colonies and this surplus honey vanished rapidly. The inland nectar flows of mid and late summer on the other hand had significantly greater effects upon the honey stored, brood reared and pollen harvested and probably produced a younger population of adult honeybees in the inland colonies. This might have improved their chances of winter survival although a subsequent examination in the spring of 1970 did not confirm this. The production of more surplus honey for the beekeeper was thus the only but very important practical benefit of these mid and late season nectar flows compared with those at the coast.

VI.4 Seasonal changes in colonies of honeybees and the relationships between important colony properties

Adult honeybees

The mean colony populations were about 18,000 (16 colonies) in late May, 37,000 (maximum) in early July and 13,000 in late September. The May and July results are very similar to the data presented by Jeffree (1955) but the population at the end of the season was in closer agreement with the optimal wintering size of a colony proposed by Jeffree and Allen (1956). It would also seem that honeybee colony populations of between 60,000 and 100,000 (Park, 1954) were unlikely in Scotland and indeed in the whole United Kingdom for single queen colonies.

Pollen stored

The pollen stored by the colonies (16) increased from about 1 kg in late May to a maximum of 2.7 kg towards the middle of the second week in June and then declined gradually to about 1 kg again in late September. The only study of pollen stored in colonies of honeybees is that of Jeffree and Allen (1957). They stated that the pollen stored in May was about 200 g, rose to a peak of about 600 g in July and then fell to about 100 g in September. There is some discrepancy between these two sets of results. A closer scrutiny of the data presented by Jeffree and Allen (1957) indicated that their colonies were "rather small", whereas the present study was carried out on strong colonies. Furthermore, Jeffree and Allen (1957) forecast from their

data that a colony of 37,000 adult honeybees should have a peak of about 1 kg of pollen in store in July, whereas the mean amount of pollen placed in store by July by the colonies used in the present study was over half as much again and even this was not the peak. The results quoted by Jeffree and Allen (1957) should perhaps be restricted to the situation in small rather than large colonies in which conditions are apparently quite different.

Brood

The mean brood population in the colonies in late May was about 50% of the maximum (21,000) achieved in early June about 18 days before the peak of the adult bee numbers and was almost negligible (604) by late September. This pattern of brood rearing was similar to that of the population of adult bees. The variation in brood population throughout the season described here was closely related to the data published by Allen (1965a) substantiating her results and simultaneously establishing that 1969 was not an abnormal brood rearing year. When these results were compared with those of Nolan (1925), who measured only 8 colonies, the pattern of brood rearing and time of maximal brood population were fairly similar although the numbers of brood reported throughout the year by him were very much higher; these differences could be due to variations between the environments or strains of honeybees.

Allen (1965a) stated that windy weather could occasionally cause a small decline in brood rearing by reducing the

foraging for food and in the present study reductions in brood by some colonies were apparently due to preparations for swarming which did not eventually occur. Bodenheimer and Ben Nerya (1937) working on one colony in Palestine found that the broodrearing cycle had 2 periods of activity (in May and September) while in California, Todd and Bishop (1941) also observed 2 distinct brood maxima (in mid-June and mid-August). Thus it would appear that, although the present results substantiate the situation for normal colonies in the maritime climate of the northern part of Britain, they would not necessarily be typical of the situation elsewhere in tropical and sub-tropical areas where apparently 2 distinct periods of brood rearing occur each season (see Section VI.1 where the reasons for different broodrearing patterns are discussed).

Honey stored

The amount of honey stored by the colonies of honeybees fluctuated throughout the active season increasing quite considerably with the spring and summer nectar flows. At other times the honey in store decreased because of the requirements for colony maintenance which have been estimated at between 0.2 and 0.7 kg per day (Ribbands, 1953). The main nectar flow patterns found in this area and elsewhere were discussed in detail in the section on nectar flows in the South-East of Scotland and the relationships between honey flows and other colony parameters are dealt with in the next section.

Brood reared and adult honeybee populations

In late May and early June a very highly significant correlation was found to exist between the amount of brood reared and the adult honeybee population. This was in agreement with Allen and Jeffree (1956) and Free and Racey (1968) who claimed that more brood was present in larger colonies in spring. It is hardly surprising because larger colonies contain greater numbers of adult bees for foraging, maintaining the brood nest temperature at 33°C (Allen and Jeffree, 1956), nursing the larvae and preparing the cells for eggs (Free, 1968). Later, soon after the brood population peak was reached, the correlation was no longer significant. Allen and Jeffree (1956) stated that this situation was caused by a few later brood peaks from the smaller colonies and swarm adjustment measures in others affecting the total correlation. However as Nolan (1925) indicated, the peak of brood production is closely related to the maximal egg laying rate of the queen and thus in this instance it would not be surprising if the numbers of brood were less significantly affected by the adult bee population as maximal brood population was attained. In July, the numbers of brood and adult bees were related in a significant but negative manner and the observations indicated that at this time brood rearing was more drastically reduced in larger colonies. This could have been caused by worker honeybees consuming eggs (Merrill, 1925) or forcing the queen to reduce her egg production by

reducing her food supply. By late August this situation had altered once again because the adult bee population was then apparently directly affecting the amount of brood reared to an extent which was almost significant. In September other effects became significant; the supply of pollen trapped and also the amount of honey in store were positively related to the brood reared.

Free (1968) stated that the brood population of colonies of honeybees was regulated by the dilution of a hormone produced by the queen so that the small colonies, having a larger concentration of the hormone, bred more intensely and for a longer time than larger colonies. It could be that larger colonies simply grow faster because they have more bees to cope with the various tasks of foraging for food, nursing and keeping the brood nest warm, and so attain the maximum egg-laying capacity of their queen earlier in the season. This simple explanation could therefore account for the differences in the breeding patterns of large and small colonies in the first half of the breeding season.

When, in the second half of the brood rearing season, the correlation between the brood numbers and the colony adult population is considered, there appears to be no simple explanation for this situation. Perhaps it is a result of a type of overcrowding as, at this time, there is a relatively high number of nurse bees who may indulge in some form of displacement activity such as eating eggs

(Merrill, 1925). Later in the season when there were smaller numbers of nurse bees one could expect colonies with larger numbers of foragers to rear more brood, as in fact they do, but the general decline in pollen availability and the colder weather discourage this behaviour.

The brood and honey in store

At certain times during the active season there was a close relationship between the amount of brood and the honey stored in the colonies. In late May for instance there was a significant negative relationship between them indicating that the honey in store was being reduced relative to the amount of brood reared and that nectar was not being gathered in sufficient quantities to minimize this effect. In June no significant effects were observed; that is, the nectar income was proving large enough to arrest the decline due to brood rearing. On 7th July 1969 a highly significant negative relationship between the amounts of brood and honey in the colonies indicated that the honey consumption was directly related to the amount of brood once more, but in August there was no significant relationship. It was obvious that honey income was having a very important effect here and that on any occasion when there was insufficient nectar income, there was a decline in the honey in store which was directly related to the amount of brood being reared. On the 23rd September it was observed that significantly more brood was being reared by colonies with more honey in store. Nolan (1925) also noted a similar phenomenon.

Brood and pollen

When the individual colony data for pollen trapped, pollen stored and brood reared were examined throughout the active season, the correlation coefficients calculated for observations on a given date did not approach significance despite the obvious relationships that must have existed between them probably because the different colonies were out of phase with each other. However when the colonies were compared with one another graphically for these features throughout the active season (Figures V.3 and V.4) they were all found to follow a somewhat similar trend especially when the pollen trapped per day was used in the comparison, and when the mean brood values on the different observation dates were correlated with the mean pollen trapped per colony per day, and the mean pollen in store per colony, the values obtained were significant ($r = 0.65^{*}$ and $r = 0.56^{*}$ respectively).

The lack of a significant correlation between the pollen trapped and stored was probably due to the effects on these factors of temporary increases in brood rearing or decreases in foraging caused by bad weather. The decline in brood rearing after the seasonal maximum was not so rapid as that of the pollen stored and trapped. This may have been due to the large amount of brood food particularly protein present in the nursing bees (Haydak, 1959) which would have to be consumed by growing honeybee larvae before pollen foraging would again require to be undertaken to sustain brood rearing.

Other workers have also found difficulty in establishing a relationship between the amount of pollen harvested and brood reared (Filmer, 1932, and Louveaux, 1958) and Free (1967) had to use rather extreme experimental methods (artificial doubling of the amount of brood in colonies) before he was successful. Cale (1967) claimed success without this trouble although he did not describe his experimental methods and Todd and Bishop (1940) indicated that the relationship existed by graphical methods. (The effects of pollen scarcity on brood rearing have already been discussed in section VI.1).

Pollen trapped and honey stored

Ribbands (1953) stated that "the proportion of pollen loads to nectar loads varies widely, being largely dependent upon both available forage and colony requirements." Thus one might expect that the two processes would hardly be related during the course of the active season except at times when the harvesting for the pollen requirements of the colony happened to coincide with nectar flows. Louveaux (1958) even described nectar gathering and pollen harvesting as two distinct processes. However Cale (1967) claimed (without describing his experimental methods in detail) that in 2 years out of 3 he had found a significant correlation between the amount of honey produced and pollen gathered by colonies. In the present study, significant correlations between honey in store and pollen harvested were found only for the observations in late September and at other times in

the active season the correlation between these two variables was very low. Thus it would appear that the time of year is most important when examining data of this type for significant correlations, and that during most of the active season low non-significant correlations existed between the pollen being harvested and the amount of honey in store in the colonies.

Pollen and honey in store

The relationship of these two factors was significant in early June, during the spring nectar flow, and in August and September, during the late season nectar flow; between these periods the relationship was not significant. It would appear then that the storage of honey in bulk made the colonies store more pollen, but that the amount of honey in store did not affect the quantity of pollen stored because there was no correlation between pollen and honey in store other than on the occasions mentioned above.

Colony size

The effect of colony size (numbers of adult honeybees) upon other phenomena associated with honeybee colonies was found to be of very great importance. Larger colonies for instance were found to rear more brood in the early part of the season (Table V.32) confirming the findings of Allen and Jeffree (1956). Presumably this is because bigger colonies have more individuals to deploy on all the various tasks than smaller ones. Larger colonies also gather more

pollen (Tables V.1 and 2) and reduce the amount of brood they are rearing sooner than smaller colonies (Table V.32). Perhaps this is really because smaller colonies are attempting to grow to a certain optimum size which the larger colonies have already attained. In addition more honey is gathered by larger colonies than smaller ones (Table V.32). This factor has been discussed by Ribbands (1953) who stated that there would be relatively more foragers available in larger colonies to harvest more honey because the relative amount of brood being reared was smaller. From this it appears that colony size is one of the most important factors in understanding the economy of a colony of honeybees and also in helping the practical beekeeper to produce large harvests of honey and pollinators for different crops . Therefore much more attention should be directed to solving the problem of the factors controlling colony size in the future than has been the case in the past.

VI.5 Nectar flows

The relationship between honey stored and total colony weight

Although it has been claimed (Oertel, 1950) that colonies of honeybees can, if weighed regularly, act as useful indicators of honey flows, no investigation of the relationship of colony weight to honey stored appears to have been undertaken. In this present study a very close relationship was demonstrated between these two factors (mean $r = 0.94$). Thus fluctuations in total weight and

changes in the weight of honey stored were closely related in colonies of honeybees. Therefore this result could justifiably be used to study the duration of a nectar flow and the amount of honey harvested from it by a colony of honeybees.

Nectar flows

The patterns of nectar production in two areas of the South-East of Scotland were characterised. On the Lothians' coast a good regular flow of nectar occurred only in early summer and was subsequently utilised to a large extent by the colony, leaving little or no surplus honey for the beekeeper at the end of the season. The virtual non-existence of a mid and late season nectar flow on the coast is not due to bad weather (Table 8.2) but the presence of suitable nectar secreting plants are essential for a nectar flow to occur. In the upland area South of the Lothians' coast a fairly good early season nectar flow was followed by much better flows in mid and late summer which produced much more surplus honey for the beekeeper. However these later nectar flows were more liable to be affected by bad weather than the early summer nectar flows as in July 1965 (Table V.35) and were, therefore, not completely dependable.

It was not possible to compare these results with others from different areas of the United Kingdom because no systematic records were available from Scotland and the only detailed English records refer to two colonies over two seasons at Rothamsted (Wafa 1954). These showed that in

1945 and 1946 the main and only nectar flow of any consequence occurred from late June to late July, a period which corresponded approximately to the mid-summer nectar flow recorded in the upland area of South-East Scotland. The "one nectar flow" season occurring at Rothamsted was very similar to the situation described by Mitchener (1947, 1955) for Manitoba, while Kettner's records from East Germany (1961) resembled the pattern of flows found in the Southern Uplands of South-East Scotland.

Attempts to correlate the changes in colony weights with the monthly weather means of rainfall, daily sunshine and maximum and minimum temperatures over three seasons (Table V.35) were unsuccessful, indicating that the mean monthly climatological data available would be of no assistance in attempting to assess nectar flow yields. Wafa (1954) also found no significant correlation between rainfall and colony weight changes. Weather undoubtedly influences nectar flows to a certain extent as in the wet summer of 1965 but, from this analysis of the situation, the effects usually appear to operate over a much shorter time scale than a month and any future studies of these relationships would be best conducted on daily weather observations.

This study of nectar flows in the area has allowed more precise advice to be given on how to obtain larger crops of honey. For instance the good regular nectar flows of the coastal area help to sustain a rapid increase

in colony population early in the season but migration to an upland area further inland is necessary in any attempt to produce a large honey crop by the end of the season. One of the most interesting features highlighted by this study is the importance of the sycamore tree (Acer pseudoplatanus) as the main source of nectar in early summer. If its numbers should ever be greatly reduced in this part of Scotland, the main source of early-nectar for honeybees would disappear.

A cheap simple machine was adapted for weighing bee-hives and this was useful in studying nectar flows. The honey production potential of other areas could be studied, using similar methods and the knowledge obtained could lead to a greater understanding of nectar flows, the plants that produce them and the conditions for optimal nectar secretion. From such a nationwide study the production of honey from colonies of honeybees in the United Kingdom could be greatly increased.

VI.6 Chemical composition of pollens

Dry matter

The results of 256 pollen dry matter determinations throughout the 1969 season as reported in the results section (Table V.36) indicated that the mean dry matter content of freshly trapped pollen was 73%. This resembled the dry matter content of dry grain (McDonald et al. 1966). Pollen which was allowed to become more moist rapidly

deteriorated due to the attack by species of Mucor fungi. The relatively dry condition of the pollen as produced by the flower may be a mechanism to ensure that it normally remains viable for a few days. This may also account for the relatively constant water content of the pollen throughout the season and also for the dry matter determinations being similar to those reported by other workers (Todd and Bretherick, 1942; Vivino and Palmer, 1944).

Pollen moisture is probably a useful source of water for colonies of honeybees in the absence of a nectar flow and rainfall. Lindauer (1955) who examined the water economy of honeybee colonies in detail did not discuss pollen moisture although he did state that the water requirements of a colony vary with the amount of brood being fed, because of the high amount of water in brood food, and that less water was required when good supplies of nectar were available. During the 1969 season the colonies of honeybees in this study gathered a mean of 3 kg of pollen in their traps and, if the traps cull about 10% of the pollen harvested (Free and Spencer-Booth, 1961), then this means that each colony on average was gathering a total of about 30 kg of pollen during the season. As about 27% of this was water, each colony was gathering about 7 kg of water with the pollen. If actually between 20 and 30% of the pollen harvested was culled, then only 10 to 15 kg of pollen would be harvested each year by one colony and this would contain about 2.5 to 3 kg of water.

When metallic traps were used it was found that the moisture content of pollen increased. This phenomenon was most marked when nectar was being harvested, and was apparently due to water condensing on the metal and dropping into the pollen in the collecting tray. Wooden traps did not appear to suffer from condensation.

Ether extract

Fatty material was not present in large quantities in any of the pollens except that of beech. Presumably this material has a function akin to that of the oil in seeds, acting as a store of energy. Fats have the disadvantage that they may deteriorate relatively rapidly as in storage within the hive but this may be of little importance to the plants because pollination normally occurs within a short time of anther dehiscence.

Some pollens, notably dandelion pollen, have oily globules on their outside coat. In these cases the oil perhaps functions as an adhesive, sticking the pollen to pollinating insects.

It has been claimed (Butler, 1949) that adult honeybees cannot digest fatty foodstuffs. This factor would not appear to be of great importance because of the relatively low quantities of fatty material in most of the pollens except of beech and perhaps crucifers where the presence of relatively larger quantities of fats might cause digestive difficulties due to the formation of 'soaps' (Davidson et al. 1959).

Other reports (Haydak and Tanquery, 1943) state that pollen lipid extracts contain certain substances which honeybees find attractive and the removal of fatty materials from pollens has adverse effects upon brood rearing.

Nitrogen

Between 2 and 5% of the pollen was nitrogen. This indicated that these pollens were potentially a relatively high source of vegetable protein with crude protein values between 16 and 39% of the dry matter. This factor may have influenced the evolutionary change that occurred when the wasp-like ancestors of bees altered their feeding habits from being carnivores to herbivores.

The highest potential suppliers of protein among the pollens studied were those of sycamore, crucifers and white clover which were also quantitavely the most important pollens harvested by the honeybees according to the traps (Tables V.11 and V.12). Beech pollen was potentially the lowest supplier of protein to honeybees with a crude protein value (16%) less than half that of sycamore pollen.

The determination of the crude protein of a foodstuff is not a very accurate method of predicting its nutritional efficiency. A more important factor influencing the nutritional quality of a protein is the amino acid composition which is considered later in this sub-section.

Carbohydrates and structural materials

About half of the pollen consisted of these substances. The largest fraction was that of the monosaccharides, glucose and fructose, which together composed about one third of the pollen dry matter. It has been stated that honeybees add some carbohydrate to help in pollen pellet formation (Casteel, 1912; Todd and Bretherick, 1942). If the only sugars present in pollen were derived from nectar or dilute honey added by honeybees then the expected ratio of glucose to fructose found in pollens should have been similar to those normally found in nectar (Wykes, 1952; Percival, 1962) or honey, but this was not the case. It would appear then from the results of the sugar analyses of pollens that a certain amount of sugar was present in the pollens naturally. Although the species investigated in this study did not lend themselves readily to hand collection for sugar analysis so that this could be verified, other pollens hand collected by Todd and Bretherick (1942) were also found to contain considerable amounts of sugars. The sugar present in pollen naturally would appear to provide the initial energy for pollen germ tube growth. It would also make a valuable contribution to the carbohydrates consumed by honeybees.

Hemicelluloses are plant structural polysaccharides which are extractable from plant cell walls by the action of dilute acids or alkalis and are, in the process, broken down into monosaccharides. Shaw and Yeadon (1966) studied

pollen membranes and found that about 3% of the membrane's dry matter consisted of an 'ill-defined xylan fraction' which was obtained by dilute sulphuric acid hydrolysis of the pollen membranes, mainly as xylose, although glucose and galactose were also present. The hemicellulose in the present examination was obtained in a similar manner and represented 7% of the dry matter of the original pollen. This hemicellulose may be digested by the honeybees but no information on this subject is available.

Cellulose, whose function is probably structural as in other plant material, was found to represent less than 1% of the pollen dry matter; this is similar to the result obtained by Shaw and Yeadon (1966) who claimed that about 3% of the pollen shell consisted of pure cellulose. Cellulose appears to be completely unusable by honeybees (Phillips, 1924).

About 16% of the original material was 'lignin', which is generally considered to be completely indigestible by insects even termites (Wigglesworth, 1953).

Starch was not detected in any of the pollens examined. In a study of 35 pollens, Parker (1926) detected starch by the iodine method in only 7 species. In many species of pollen, as has already been indicated, there is probably enough mono-and oligosaccharides to supply the energy for pollen germ tube germination.

Pollen minerals

Insect nutrition remains a neglected subject and this

is indeed the case of the honeybee (Haydak, 1970). It is therefore difficult to evaluate the nutritional worth of the constituents of pollen for the honeybee in detail although some remarks may serve to illustrate their function or possible use in the insect.

About 3% of the pollen dry matter was ash and almost half of this ash consisted of the minerals which were determined. An analysis of variance of the mineral contents of the different pollens examined indicated that there were significant differences between the manganese and calcium composition of some of the pollens but not between the sodium, magnesium and potassium contents. Phosphorus functions biochemically in the formation of intermediate compounds in carbohydrate metabolism. The honeybee metabolises relatively large amounts of carbohydrate during its lifetime. From the present analyses of the pollens examined they would appear to be potentially able to supply sufficient phosphorus to meet the metabolic demands of the honeybee provided, of course, that the phosphorus was present in an available form. Calcium is found in quantity within crystals in the honeybee gut wall and appears to be part of a digestive process for neutralising the acidity of honey (Koehler, 1920). The calcium required for this function could be supplied by pollen and particularly that from crucifers and heaths. Magnesium is required by honeybees to activate certain enzymes, for example α-ketoglutaric dehydrogenase (Hoskins et al. 1956). Manganese was found

in relatively high concentration in heath pollens probably because, in the acidic soils in which heaths tend to be found, the availability of this element is greater than in neutral or basic soils. Manganese is commonly found activating oxidative phosphorylating enzyme systems. Potassium and sodium were found in pollens in concentrations rather similar to those in honey. Pollen will not then be the main supplier of these elements to honeybees. These elements appear to be essential in living systems; potassium and sodium occur predominantly in intracellular and extracellular sites respectively.

The gross energy of pollen

The gross energy values of the samples of pollen were relatively high with a mean value of approximately 5,500 Calories per gram. Pollen is therefore a very concentrated source of energy even when compared, on a dry matter basis, with honey which has a gross energy value of approximately 3,600 Calories per gram (McCance and Widdowson, 1945). A calculation based on the gross energies of the mean crude protein, ether extract and the remainder (classed as equivalent in energy value to a similar quantity of glucose) did not account for all the pollen energy although for most foodstuffs this approximation is usually very similar to the gross energy values determined by calorimetry (Table VI.2). It would appear that the bond energy values of the pollenin of the pollen grain wall were considerably higher than those of glucose.

TABLE VI.2

Calculation of gross energy of pollen

	Dry matter %	Gross energy values
Pollen mean crude protein value	26	1530
Pollen mean ether extract value	4.8	448
Pollen mean value for remainder (as glucose)	69.1	2584
		4562 Cals/g

Deoxyribonucleic acid

This fraction was examined to determine whether a significant quantity of nucleic acid was present in any of the pollens which might affect the assessment of crude protein calculated from the formula 6.25 x N. The deoxyribonucleic acid (DNA) content of the pollen was less than 0.5% of the dry matter for all the main pollens. This agreed fairly closely with determinations of total nucleic acid of some pollens which lay between 0.2 and 1.5% of the dry matter (Sosa - Bourdouil, 1949). It also indicated that nucleic acid nitrogen would not affect the Kjeldahl method of estimating nitrogen.

The amino acids

Pollen: Although variations were observed between the amino acid content of the pollens, analysis of variance showed that most of these differences were not significant except for serine, cystine and histidine. Generally the

results obtained were similar to those of Weaver and Kuiken (1951) who examined the essential amino acids in pollen species from the U.S.A.

The proportions of the different amino acids in the two sets of results mentioned above were very similar irrespective of the plant species, but variation in the actual amount of crude protein in them was quite large, and from the present study it would appear that estimates of pollen crude protein could be used to evaluate biologically the protein nutritive value of the pollen income for honeybees.

A comparison of the proportional relationship of the essential amino acid composition of the pollens with the essential amino acid requirement of honeybees (Groot, 1953) indicated that all the pollens examined, except heath pollen which was relatively low in methionine, were present in proportions above the relative minimum values for adequate honeybee nutrition, and therefore appeared to be almost ideal potential sources for the amino acids required by the honeybee.

When the mean amino acid content of the pollens was compared with that of royal jelly (Weaver and Kuiken, 1951) it was found that there were no significant differences. A comparison of the amino acid analyses of the pollens with that of materials used in the formulation of pollen substitutes indicated that there were no great differences between these two groups of substances either (Table VI.2).

It is perhaps useful to give some attention to the phenomenon of nutritional interaction of the amino acids. It was thought that, since amino acids entered into a variety of metabolic pathways, excess amounts of these substances not used for protein synthesis were degraded by normal pathways of intermediate metabolism. However it is now acknowledged that surpluses of particular amino acids may impose limitations on the growth of animals commensurate with their deviation from the ideal requirements and in certain instances these effects can be quite noticeable (Lewis, 1965). These effects appear to occur in certain pairs of the amino acids, for example, arginine and lysine, as well as leucine and iso-leucine, leucine and valine, and threonine and tryptophan (Lewis and D'Mello, 1967), when the amount of one of them present in the diet is much higher than the other. In the present assessment of the amino acids of the main pollens harvested in this area, there were no wide fluctuations between any of the members of these particular amino acid pairs and therefore it was unlikely that any of these interactions occurred in the utilisation by the worker honeybee of these pollens. However in some of the substances used as pollen substitutes it is possible that interactions could occur and thus account for certain nutritional inadequecies of these materials. In casein, for example, there is a relatively high amount of lysine compared with arginine which might cause nutritional interactions. Other differences in

performance between these pollen substitutes could probably be ascribable to the other factors such as vitamins, lipids and perhaps minerals (Haydak, 1970).

Honeybee: Although nutritional balance studies were outwith the scope of this study, it was felt that the nutritional evaluation of the pollen amino acids could be extended by using as a yardstick for comparison the method of carcass analysis developed by Mitchell (1950; 1964) and Williams et al. (1954). It is based on the assumption that carcass amino acids and food amino acids should be similar. The analysis of variance of the amino acids of four adult worker honeybees in the present study indicated no significant differences between the quantities of the amino acids determined except glycine, alanine and lysine. In fact, as quite wide variations in the amino acids concentrations occur generally in insect blood even within the same species (Gilmour, 1961) it is perhaps surprising that the similarities obtained were so great. It should perhaps be mentioned that as uric acid (the principal end product of nitrogen metabolism in insects) is partly converted to glycine by the acid hydrolysis procedure used in determining the amino acids (Shannon, 1971) varying amounts of uric acid could perhaps account for the differences in glycine between the different analyses.

When the mean amino acid values of the honeybee carcasses were compared with those mean values obtained from the various pollens (Table VI.3) only the amino acids,

TABLE VI.3

A comparison of the essential amino acid contents of honeybees and some of their natural and artificial foodstuffs. (All amino acids as g/16g N)

	Mean pollen values[1]	Royal jelly[2]	Soya bean flour[3]	Casein[4]	Whole egg[5]	Honeybee requirements[6]	Worker honeybee contents[7]
Arginine	5.0	5.1	7.7	3.4	6.2	3.0	4.2
Histidine	2.2	2.2	2.3	2.7	2.4	1.5	2.3
Iso-leucine	4.6	5.3	5.3	5.7	5.8	4.0	4.7
Leucine	7.1	7.7	8.0	8.7	9.0	4.5	7.5
Lysine	5.2	6.7	6.6	6.9	7.5	3.0	4.6
Methionine	2.2	1.9	1.4	2.8	3.3	1.5	1.3
Phenylalanine	4.6	4.1	5.1	4.8	4.8	2.5	3.2
Threonine	4.8	4.0	3.9	3.9	4.7	3.0	3.6
Valine	5.5	6.7	5.3	6.6	6.8	4.0	5.9
Totals	41.2	43.7	45.6	45.5	50.5	27.0	37.3

(1 and 7, present study; 2, Weaver and Kuiken, 1951; 3 and 5, Kuiken and Lyman, 1949; 4, Cole, 1950; 6 , Groot, 1953).

methionine, threonine and serine were found to be significantly different, indicating that, on the basis of carcass analysis, these pollens were almost ideal food substances for the worker honeybee. Crude protein values of pollens were useful for evaluating their nutritional worth. Interactions might occur with casein which is commonly used in formulating substitutes for pollen and so attention should be paid to this factor when casein is being used in studying the protein metabolism of the honeybees.

VI.7 Honey chemistry

Honey cations

The range of concentrations of Mg and Na was similar and small, that of Ca about four times greater and of K ten times. All distributions of the concentrations were of the skew type (Figures V.13, 14, 15 and 16), the greater number of values occurring in the lower part of the range. Na and K had very similarly shaped distribution curves although the ranges of the values were very different. The results of the present study were comparable with those of Schuette et al. (1932, 1937, 1938, 1939) for K and Mg but for Na and Ca the range was less than half, and double respectively.

When the relationship between the ions was investigated by correlation and multiple regression techniques it was observed that the ion pairs, K and Mg, and Na and Mg respectively were the most and the least closely related cations in

honey and these relationships were not greatly affected by the amounts of the other cations present.

Since honeybees make honey from nectar by inversion of the greater part of the sucrose to glucose and fructose and the reduction of the water content from an average value of about 60 - 65% to a value of approximately 17 - 25% chemical analysis of a honey should give a good indication of the parent nectar from which it was derived provided that account is taken of these changes in water and sugar (Butler, 1949). Thus the ratios of the different cations in nectar and honey should be similar and the relationships between them should provide valuable information about the mineral content of nectar.[1]

(An evaluation of these cations for honeybee nutrition has already been made in the discussion of pollen minerals in Section VI.6).

[1] Provided no differential loss takes place in the conversion of nectar to honey.

VII CONCLUSIONS

The mean active pollen harvesting season for honeybees in the South-East of Scotland is fairly short (107 to 120 days) and individual colonies gather very few pollen types: the general mean in 1969 was 14 types. Sycamore is the dominant source of pollen (38% - 1969 harvest) with white clover (12% - 1969 harvest) and crucifer pollen (10% - 1969 harvest) as the other important types gathered. Of the 32 types of pollen harvested from all sites in 1969, 21 were in amounts representing less than 1% of the total. Pollen harvests can be compared using the concept of index of diversity which has been adapted here for this purpose; the low values of this index which were found show that little of the available flora is being used by honeybees. Mixed woodland is the habitat from which honeybees collect relatively the most pollen (67% - 1969 harvest); coniferous woodland is of little value for pollen collection; meadowland (21% - 1969 harvest) and arable land (12% - 1969 harvest) are fairly similar to each other in the amounts of pollen harvested from them by honeybees.

There is a very high correlation between the colony weight and the honey stored in a colony throughout the season (mean $r = 0.95$). There are at least 2 distinct nectar flow patterns in the South-East of Scotland; these produce different effects on colonies of honeybees. The coastal nectar flows are generally very good in spring but little honey is produced there during the remainder of the

season, whereas in the upland areas the spring nectar flows are not so intense, but the mid and late-season nectar flows are very much better. The storing of greater amounts of pollen and honey in early summer are the only significant effect on colonies that experience the better coastal nectar flows of that time of year. The substantial mid and late-seasonal nectar flows of the upland areas, on the other hand, are accompanied by an increase in brood rearing, pollen gathering, a transient increase in the adult population and above all by a greater amount of honey stored (36 kg) compared with the coastal colonies (11 kg) which did not experience a nectar flow then. There was no difference between the survival rates of the two groups of colonies during the winter. No significant difference was observed between the number of pollen types gathered on upland and coastal sites, and, of the more important pollens harvested by the bees, only hawthorn was gathered at the coast in quantities which were significantly larger than those of the upland sites.

The measurement of the numbers of bees and brood, and the amounts of honey and pollen stored, and the pollen trapped throughout the season showed that colony size is very important in colony development. Large colonies rear more brood in the early part of the season, cease rearing brood earlier, and above all store more honey by the end of the season, than smaller colonies. More attention should be paid to the factors influencing the size of

honeybee colonies in any future study. The large decrease in pollen harvesting after midsummer, as shown by the pollen trap returns, is probably caused by the large protein reserve of the nurse bees whose numbers would be maximal then.

Pollen traps did not produce drastic effects upon colonies; the only measurable differences were the storing of slightly less honey and pollen in June, a reduction in the numbers of adults in trapped colonies in August, and in the numbers of colonies which survived until the following spring. There was however no apparent effect upon the amount of brood being reared in any of the trapped colonies at any time. Pollen traps were found to harvest a variable percentage of the total amount of pollen gathered by colonies of honeybees: relatively more pollen being trapped at times when pollen harvesting was most intense.

Except for pollen from heaths which was relatively low in methionine, but not significantly so, the essential amino acids considered were present in the pollens examined in proportions above the relative minimum values. The relative proportions of the amino acids in the main pollens examined were so similar, with the exceptions of serine, cystine and histidine, that it was felt that the crude protein values of the pollens (range, 35% sycamore - 16% buttercup) could be used as an estimate of the amount of useful protein that each of them would be able to supply. Furthermore, a comparison of the amino acids from the acid

hydrolysis of honeybee carcasses with the amino acids from these pollens indicated that they were so similar to each other that the pollens appeared to be almost an ideal food for supplying these amino acids to honeybees. The pollens from sycamore, crucifers and white clover, which were those gathered in greatest amount, were quantitatively the best sources of these amino acids, and casein, which is frequently used as a pollen supplement was shown to be liable to produce interactions between the amino acids lysine and arginine.

Pollen could also be a useful source of water (27% of the fresh weight) for honeybees when moisture was otherwise scarce. In beech pollen the relatively high amount of lipid (11.8% of the dry matter) might lead to digestive troubles from the formation of soaps. The cations K and Mg, of honey, were the most closely related cations and Na and Mg were the least, while the Na concentrations were the most and the Mg ions were the least affected by other ions. In the pollens examined Mn was particularly high in heaths (209 ppm) and significant differences were also found between the Ca content of pollens which was highest in crucifers and heaths and also that of Mg which was highest in buttercups and crucifers. Generally however, pollen appeared to be a relatively better source of these minerals than honey for the honeybee. The gross energy of pollen was relatively high (5,500 Calories per gram).

The condensation of moisture on metallic pollen traps was found to wet the pollen so much that it was rapidly attacked by Mucor fungi and was consequently difficult to preserve and identify; wooden traps were free from this fault. A visual method of estimating the number of honeybees (Jeffree, 1956) and a graded wire grid for measuring the amount of pollen brood and honey in combs (Jeffree, 1958) were both found to give satisfactory results.

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APPENDIX 1

The floral composition of the sites at Penicuik, Bush, Broadwood and Maggie's Waas

Latin name	English name	Area[1] A	B	C	D
1. Penicuik House site:					
(a) Tree layer					
Acer pseudoplatanus	Sycamore			A	
Fagus sylvatica	Beech			O	
Larix decidua	Larch			F	
Picea abies	Norway spruce			O	F
Pinus spp.	Pine			O	F
Prunus avium	Wild cherry			O	
Quercus spp.	Oak			F	
Tilia vulgaris	Lime			O	
Ulmus spp.	Elm			O	
(b) Shrub layer					
Alnus glutinosa	Alder			LF	
Crataegus monogyna	Hawthorn			A	
Ligustrum vulgare	Privet			LF	
Rhododendron ponticum	Rhododendron			LA	
Rubus fruticosus	Blackberry			LF	
Rubus idaeus	Raspberry			LA	
Sambucus nigra	Elderberry			LF	

[1] See key at the end of Appendix 1.

Latin name	English name	Area A	B	C	D
(c) Field layer					
Achilea millefolium	Yarrow		F		
Bellis perennis	Daisy		A		
Chamaenerion angustifolium	Rosebay willow-herb		O	LA	
Cirsium spp.	Thistle		LO	LO	
Echium vulgare	Viper's bugloss		LO		
Erica spp.	Heaths		LF		
Filipendula ulmaria	Meadow sweet		LF		
Lotus spp.	Birdsfoot trefoil		A	O	
Melilot spp.	Melilot		O	LO	
Papaver spp.	Poppy		O		
Ranunculus spp.	Buttercup	F	LA	LF	
Raphanus raphanistrum	Wild radish	A			
Rumex spp.	Dock	O	F	F	
Sinapis arvensis	Charlock	A			
Succisa pratensis	Devil's bit scabious		O	O	
Taraxacum officinale	Dandelion		LF	LO	
Trifolium repens	White clover		A	O	
Umbelliferae	Umbells		F	O	
Vicia spp.	Vetch		F	O	
2. Bush House site:					
(a) Tree layer					
Acer pseudoplatanus	Sycamore			A	
Fagus sylvatica	Beech			F	

Latin name	English name	Area A	B	C	D
Tree layer contd.					
Larix decidua	Larch			O	LA
Picea abies	Norway spruce			O	LA
Pinus spp.	Pine			O	LA
Prunus spp.	Wild cherry			O	
Quercus spp.	Oak			F	
Tilia vulgaris	Lime			O	
Ulmus spp.	Elm			O	
(b) Shrub layer					
Alnus glutinosa	Alder			LF	
Ilex aquifolium	Holly			O	
Rhododendron ponticum	Rhododendron			LF	
Rubus fruticosus	Blackberry			LF	
Rubus idaeus	Raspberry			LA	
Sambucus nigra	Elder			LO	
Sarothamnus scoparius	Broom			LF	
Ulex europaeus	Gorse			LF	
(c) Field layer					
Achilea millefolium	Yarrow		LF	O	
Allium ursinum	Ransomes			LA	
Anthriscus sylvestris	Cow parsley		LF	O	
Bellis perennis	Daisy		A	O	
Chamaenerion angustifolium	Rosebay willow-herb		LO	LA	
Cirsium arvense	Thistle, creeping		O	O	

Latin name	English name	Area A	B	C	D
Field layer contd.					
Cirsium vulgare	Thistle, spear		O	O	
Erica spp.	Heaths		LF		
Filipendula ulmaria	Meadowsweet		LF		
Gallium cruciata	Crosswort		LA	O	
Gallium verum	Lady's bedstraw		F	O	
Heracleum spondylum	Hogweed			O	
Lathyris pratensis	Meadow pea		O	O	
Lotus spp.	Birdsfoot trefoil		F	O	
Myrrhis odorata	Sweet Cicely		F	O	
Potentilla anserina	Silverweed		LF	O	
Prunella vulgaris	Self heal		LA	O	
Ranunculus spp.	Buttercup	O	LA	LA	
Raphanus raphanistrum	Wild radish	F			
Silene spp.	Campions	O	O	O	
Sinapis arvensis	Charlock	A			
Taraxacum officinale	Dandelion		LF	O	
Trifolium repens	White clover		A	O	
Veronica spp.	Speedwells		F	F	
Vicia craca	Tufted vetch		O	O	
Vicia sepium	Bush vetch		O	O	
Viola tricolor	Heartsease		O	O	

Latin name	English name	Area A	B	C	D
3. Broadwood site:					
(a) Tree layer					
Acer pseudoplatanus	Sycamore			F	
Aesculus hippocastanum	Horse chestnut			O	
Fagus sylvatica	Beech			O	
Fraxinus excellsior	Ash			O	
Larix decidua	Larch				F
Pinus spp.	Pine				F
Prunus spp.	Wild cherry			O	
Quercus spp.	Oak			O	
Ulmus spp.	Elm			O	
(b) Shrub layer					
Alnus glutinosa	Alder			O	
Crataegus monogyna	Hawthorn			F	
Hippophae rhamnoides	Sea buckthorn			LA	
Ligustrum vulgare	Privet			LF	
Rubus fruticosus	Blackberry			F	
Rubus idaeus	Raspberry			LA	
Sambucus nigra	Elder			F	
(c) Field layer					
Artemesia vulgaris	Mugwort			O	
Astragulus danicus	Purple milk vetch			LO	
Bellis perennis	Daisy		A	F	
Campanula spp.	Harebell		LO	O	

Latin name	English name	Area A	B	C	D
Field layer contd.					
Carduus spp.	Thistle		LA	O	
Centaurea spp.	Knapweed		LF	O	
Cerastium holosteoides	Mouse eared chickweed	F	O	LO	
Chamaenerion angustifolium	Rosebay willow-herb			LF	
Cirsium spp.	Thistle		LA	O	
Echium vulgare	Viper's bugloss		O	A	
Erodium cicutarium	Common storksbill		F	F	
Filipendula ulmaria	Meadowsweet		LO	LO	
Glechoma hederacea	Ground ivy		O	O	
Hieracium pilosella	Mouse ear hawkweed		F	O	
Papaver spp.	Poppy	O	O	O	
Pentaglottis sempervirens	Green alkanet			O	
Trifolium repens	White clover		A	O	
Lotus spp.	Birdsfoot trefoil		A	LF	
Melilot officinalis	Common melilot		O	LO	
Myosotis spp.	Forgetmenot		F	LA	
Prunella vulgaris	Self heal	O	A	LO	
Raphanus raphanistrum	Wild radish	F	O		
Rubus fruticosus	Blackberry		O	LF	
Rubus idaeus	Raspberry			LO	
Senecio jacobea	Common ragwort		O	O	
Knautia arvensis	Field scabious		F	LF	
Scrophularia nodosa	Common figwort			O	
Silene alba and S. dioica	Campions, white and red	O	O	LO	

Latin name	English name	Area A	B	C	D
Field layer contd.					
Sinapis arvensis	Charlock	F			
Solanum dulcamara	Bittersweet			LF	
Thymus drucei	Wild thyme		O	O	
Umbelliferae	Umbells		F	F	
Veronica spp.	Speedwells		O	LA	
Vicia spp.	Vetches		F	O	
Viola spp.	Violets		F	F	
4. Maggie's Waas site:					
(a) Tree layer					
Acer pseudoplatanus	Sycamore			F	
Aesculus hippocastaneum	Horse chestnut			O	
Betula spp.	Birch			LF	
Fagus sylvatica	Beech			F	
Quercus spp.	Oak			F	
Tilia vulgaris	Lime			O	
Ulmus spp.	Elm			O	
(b) Shrub layer					
Crataegus monogyna	Hawthorn			F	
Ilex aquifolium	Holly			O	
Rhododendron ponticum	Rhododendron			LF	
Rosa canina	Wild rose			LF	
Rubus fruticosus	Blackberry			O	
Sambucus nigra	Elderberry			F	
Taxus baccata	Yew			O	

Latin name	English name	Area A	B	C	D
(c) Field layer					
Chaerophyllum temulentum	Rough chervil			O	
Chamaenerion angustifolium	Rosebay willow-herb			LF	
Echium vulgare	Viper's bugloss		LF	O	
Filipendula ulmaria	Meadowsweet		LF		
Geum urbanum	Herb bennet		O	LF	
Hieracium spp.	Hawkweeds		F	O	
Lamium album	White dead nettle	O			
Lotus spp.	Birdsfoot trefoil	F	O	O	
Myosotis spp.	Forgetmenot	O	O	O	
Papaver spp.	Poppy	LF	O		
Ranunculus spp.	Buttercup	O	LF	LF	
Raphanus raphanistrum	Wild raddish	A			
Sinapis arvensis	Charlock	A			
Solanum dulcamara	Bittersweet			LF	
Trifolium repens	White clover		A		
Umbelliferae	Umbells		O	F	
Veronica spp.	Speedwells		O	LA	
Vicia spp.	Vetches		F	O	

KEYS

1. Land use
   - Area A = arable crops
   - Area B = pasture and moorland
   - Area C = mixed woodland
   - Area D = conifers

2. Species frequency
   - A = abundant
   - F = frequent
   - O = occasional
   - L = prefix meaning "locally".

APPENDIX 2

Brood reared by colonies 1969

The brood reared by 16 colonies in 1969 was calculated for the period between 22nd May and 23rd September (Table 2.2) and the correlation between it and the total pollen trapped (Table 2.1) calculated, $r = -0.1$. The pollen required for the amount of brood reared (based upon the relationship proposed by Todd and Bishop, 1940) was also calculated (Table 2.2) and compared with the actual amount of pollen trapped (d.m.) in order to give an estimate of trap efficiency on different colonies throughout the active season. The pollen dry matters calculated for Table 2.2 were based upon the mean percentage dry matters of the different site collections in Table V.36.

TABLE 2.1

Total brood reared and pollen trapped between 22nd May and 23rd September 1969

Colony	Brood reared	Pollen trapped (g)[1]
9	75,348	2237
38	80,203	3045
39	112,155	1901
11	70,518	3086
50	62,875	3413
32	121,982	1854
25	72,939	3917
28	83,359	6821
13	54,289	3120
27	64,683	1682
56	65,326	1783
51	74,211	2633
48	88,334	2863
12	32,874	3987
30	50,871	3694
35	47,668	1795
Mean ± S.e.m.	77,800 ± 7,700	

[1]Figures taken from Appendix 7, Table 7.3

TABLE 2.2

Brood reared (a), pollen required (g, dry matter) to rear this brood (b), pollen (g,d.m.) trapped (c) and c as a % of b. (See note at end of table)

Colony		21-22 May 4 June	4 June 11 "	11 June 23 "	23 June 7 July	7 July 20 Aug.	20 Aug. 23 Sep.
9	a	9,760	6,528	14,888	12,256	24,915	7,001
	b	976	653	1,489	1,226	2,492	700
	c	286	399	232	74	651	0
	d	34	61	16	6	26	0
38	a	15,218	8,759	15,671	6,604	18,385	15,566
	b	1,522	876	1,567	660	1,839	1,567
	c	472	513	366	88	589	290
	d	31	59	23	13	32	14
39	a	10,503	7,092	11,094	11,599	44,383	27,484
	b	1,050	709	1,109	1,600	4,438	2,748
	c	75	381	109	96	591	137
	d	7	54	10	6	13	5
11	a	14,045	8,798	13,302	4,600	16,553	13,220
	b	1,405	880	1,330	460	1,655	1,322
	c	565	505	253	154	753	36
	d	40	57	19	33	46	3
50	a	8,050	4,926	10,365	9,427	24,577	5,530
	b	805	493	1,037	943	2,458	553
	c	662	816	284	183	523	41
	d	82	166	27	19	21	7

32	a	14,820	9,480	17,526	13,412	48,311	18,433
	b	1,482	948	1,753	1,341	4,831	1,843
	c	436	372	1,150	78	269	83
	d	29	39	7	6	6	5
25	a	10,296	6,544	11,722	9,476	27,565	7,336
	b	1,030	654	1,172	948	2,757	734
	c	580	893	244	158	910	80
	d	56	137	21	17	33	11
28	a	10,273	6,785	14,942	13,386	32,480	5,493
	b	1,027	679	1,494	1,339	3,248	549
	c	1,241	1,383	464	333	1,542	33
	d	131	203	31	25	47	6
13	a	12,320	7,138	13,096	8,273	13,276	186
	b	1,232	714	1,310	827	1,328	19
	c	635	842	317	164	279	0
	d	52	118	24	20	21	0
27	a	7,873	5,838	13,225	12,808	24,939	0
	b	787	584	1,326	1,281	2,494	0
	c	325	564	62	105	191	0
	d	41	97	5	8	8	0
56	a	16,123	9,829	15,839	5,441	11,373	6,721
	b	1,612	983	1,584	544	1,137	672
	c	445	422	168	108	181	0
	d	28	43	11	20	16	0

TABLE 2.2

Colony		21-22 May 4 June	4 June 11 "	11 June 23 "	23 June 7 July	7 July 20 Aug.	20 Aug. 23 Sep.
51	a	14,176	8,039	14,038	10,173	22,963	4,822
	b	1,418	804	1,404	1,018	2,296	482
	c	577	684	240	119	336	0
	d	41	85	17	12	15	0
48	a	17,741	9,008	17,879	12,670	25,469	5,567
	b	1,774	901	1,788	1,267	2,547	557
	c	236	745	381	47	619	54
	d	13	83	21	4	24	10
12	a	6,287	4,236	7,713	4,344	7,855	2,439
	b	629	424	771	434	786	244
	c	524	739	337	285	885	11
	d	83	173	44	66	113	5
30	a	5,152	3,830	11,347	9,450	18,336	2,756
	b	515	383	1,135	945	1,834	276
	c	655	633	406	321	658	0
	d	127	165	36	34	36	0

35	a	6,977	4,635	10,227	7,800	15,590	2,439
	b	698	464	1,023	780	1,559	244
	c	271	348	162	84	435	0
	d	39	75	16	11	28	0
Mean values	d	45	92	24	17	25	6

General seasonal mean calculated from above data = 31%; $\left(\frac{\Sigma c}{\Sigma d} \times \frac{100}{1}\right)$

Note: As honeybees are 21 days as brood before hatching as adults the number of bees reared between two observation days would be:-

$$\frac{\text{No. of brood on observation day 1} + \text{No. of brood on observation day 2}}{2} \times \frac{1}{21} \times A$$

Where A is the number of days between observations.

APPENDIX 3

Pollen collection from traps 1963-1965 - 6 colonies

Note:

1. All weights (g) in the upper part of each box are fresh weights.
2. All percentages are in the lower part of each box.
3. All figures are rounded off to the first decimal place.
4. The order in which the species are arranged is mainly that in which they were collected although variations occur due to the behaviour of the honeybees and the effects of season.

TABLE 3.1 Colony X 1963

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Rubus spp.	Ranunculus spp.	Trifolium repens	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 21	12.0 92	0.3 2	0.8 6									13
22	5.9 49	0.2 2	5.9 49									12
23	13.5 45	0.9 3	13.8 46					1.8 6				30
26	23.8 66		11.5 32					0.8 2				36
27	13.7 72	0.2 1	4.2 22					1.0 5				19
28	10.1 46	1.5 7	7.5 34					2.9 13				22
29	3.0 75	0.0 1	0.5 12					0.5 12				4
30	1.4 71	0.0 2	0.4 20					0.1 7				2
31	2.5 83	0.0 1	0.5 15					0.0 1				3
June 2	17.4 80		5.2 20									22.6
3	11.0 100											11
4	3.5 99							0.1 1				3.5
5	2.4 98							0.0 1				2.5
6	5.9 98	0.1 1									0.1 1	6
8	45.7 83	8.8 16									0.6 1	55
10	6.0 100											6
11	22.0 100											22
12	9.9 27.1			23.1 63.1	3.6 9.8							36.6
14	4.2 20			16.8 80								21
16	20.4 86	1.2 5					2.2 9					23.8

Colony X 1963

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Rubus spp.	Ranunculus spp.	Trifolium repens	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Unknowns	Totals
June 19	1.6 39	1.4 36			0.6 16	0.3 8						0.0 1	4
21	1.9 12	11.2 70			2.9 18								16
23		11.5 64			2.2 12	1.8 10	0.6 14						16
24		2.3 82			0.7 18								3
26		9.0 75			0.8 7	1.1 9		1.1 9					12
July 5		8.4 31			7.6 28	9.7 36	1.4 5						27
7		3.3 10			3.3 10	26.4 80							33
8		0.4 25			0.8 50	0.4 25							1.5
9		3.3 30			2.2 20	5.5 50							11
12		2.7 34			3.6 44.2	1.1 13.4	0.7 8.4						8
15		16.0 59			4.0 15	6.8 25				0.3 1			27
16		20.5 85			1.7 7	1.8 8							24
18		3.6 91			0.2 5	0.2 4							4
22		64.0 75				17 20				4.0 5			85
23		2.6 65			0.2 5		0.2 5		1.0 25				4
24		0.2 10							1.8 90				2
27		3.3 47				2.8 40			0.9 13				7
29		2.8 14				133 75		1.1 6	0.9 5				18
Aug. 2		6.9 16				31.0 72	1.7 4			3.4 3			43
5		1.5 74				0.2 11	0.2 8			0.1 7			2
8		37.6 80				9.4 20							47

Colony X 1963

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Rubus spp.	Ranunculus spp.	Trifolium repens	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
Aug. 12		5.5 25				13.2 60			3.3 15			22
15		0.4 3				11.8 84	0.4 3		1.4 10			14
18						6.3 90			0.7 10			7
26						25.7 99			0.3 1			26
28						0.7 10			3.5 50		2.8 40	7
29		3.8 63				0.6 10			1.6 27			6
Sept. 9									2.7 90		0.3 10	3
13									1.8 90		0.2 10	2
Totals	50.2 28.5	35.5 28.3	50.2 6.0	39.9 4.8	34.2 4.1	187 22.5	7.2 0.9	9.3 1.1	19.9 2.4	7.8 0.9	4.0 0.5	832.5

TABLE 3.2 Colony Y 1963

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Betula spp.	Prunus/ Pyrus	Rubus spp.	Sarothamnus scoparius	Crataegus monogyna	Quercus spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 21			4 100															4
22	0.9 15		5 83	0.1 2														6
23			19.7 94	1.3 6														21
26	22.1 47		22.5 48	2.4 5														47
27	29.7 53		17.4 31	6.7 12										2.2 4				56
28	15.6 18		55.8 64	15.6 18														87
29	6 25		15.6 65	2.4 10														24
30	2.2 20		7.1 64	1.7 15										0.1 1				11
31	8.8 22		27.6 69	3.2 8										0.4 1				40
June 2	69.7 75		18.6 20	2.8 3										1.9 2				93
3	8.4 42		4 20	0.4 2		6.2 31								1 5				20
4	5.9 59				0.2 2	3.7 37								0.2 2				10
5	2.9 36	0.1 1				5 63												8
6	3.2 18					12.6 70								1.4 8			0.7 4	18
9	69.9 55					50.8 40								6.4 5				127
10	5.3 38					8.4 60								0.3 2				14
11	5.5 7					55.3 70	15 19			2.4 3				0.8 1				79
12	2.6 12					12.1 55		3.3 15	1.3 6			2.6 12						22
14	1.4 6					13.2 55	4.3 18	5 21										24
16		3.6 8				32.5 74	6.2 14				0.9 2			0.9 2				44
19		3.5 87				0.3 8								0.2 5				4
21		14.9 93				0.2 1				0.8 5				0.2 1				16
23		24.1 75.3					5.3 16.5			2.6 8.2								32

Colony Y 1963

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Betula spp.	Prunus/Pyrus	Rubus spp.	Sarothamnus scoparius	Crataegus monogyna	Quercus spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
June 24		3.7 73								1.1 22	0.3 5							5
26		27.5 79								6.3 18	1.2 3							35
July 5		24.8 46								23.8 44	5.4 10							54
7		32.1 51								26.5 42							4.4 7	63
8		0.9 30								1.7 55	0.5 15							3
9		18.4 34								29.2 54	6.5 12							54
12		7.1 21								19.7 58	5.8 17		1.4 4					34
15		3.1 9								20.7 61	7.8 23					2.4 7		34
16		4.9 8								32 52	19.7 32					4.9 8		61.5
18		0.4 6								1.3 18.5	3.6 52		0.4 6			1.2 17.5		7
22		118 52								68 30	31 14					9 4		226
23		1.4 24											4.4 73			0.2 3		6
24		3.0 99									0 1							3
27		0.6 3								0.2 1	18.3 87		1.9 9					21
29		5.3 16									24.8 75		1 3	2 6				33
30		3.3 10								2.6 8	26.4 80		0.6 2					33
Aug. 2		29.6 40									14.8 20		14.8 20			14.8 20		74
5		3.9 77									0.5 9		0.4 7			0.4 7		5
8		18.4 34									20.5 38				15.1 28			54

Colony Y 1963

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Betula spp.	Prunus/ Pyrus	Rubus spp.	Sarothamnus scoparius	Crataegus monogyna	Quercus spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
Aug. 12		9.2 61									4.7 21		0.3 2		0.9 6			15
15											12 100							12
18											9 100							9
21											2.7 90				0.3 10			3
26											25 50						25 50	50
28																		0
29											9 32				2 7		16.8 61	27.8
30																		0
Totals	260.2 15.1	361.5 20.9	197.3 11.4	36.6 2.2	0.2 0.0	200.3 11.6	30.8 1.8	8.3 0.5	1.3 10.1	238.9 13.8	250.2 14.5	2.6 0.2	25.2 1.5	17.9 1.0	18.3 1.1	32.9 1.9	46.9 2.7	1729.3

TABLE 3.3 Colony F 1964

	Acer pseudoplatanus	Cruciferae	Prunus/Pyrus	Rubus spp.	Sarothamnus scoparius	Ranunculus spp.	Caryophyllaceae	Trifolium repens	Umbelliferae	Compositae	Chamaenerion angustifolium	Ericaceae	Totals
May 18	48.8 95.7									2.2 4.3			51
22	19.4 97									0.6 3			20
27	21 100												21
June 1	49.4 91.5	4.6 8.5											54
10	65.9 91.5	2.2 3		4 5.5									72
19	3.9 4.5	53.1 61.8	0.2 0.3	1.1 1.3	27.5 32							0.2 0.3	86
24		50 73.5	0.5 0.8	1 1.5	4 5.9	12 17.6	0.5 0.8						68
26		32.5 78				7.5 18		2.0 5					42
July 4		36 74				7 14		4.5 9		1.5 3			49
13		18.1 37		1 2		8.8 18		6.4 13	0.5 1	2.0 4		12.3 25	49
20		28 85							1 3	1.0 3	3 9		33
27		4 10					1.5 4	25.5 64		0.5 1	8.5 21		40
Aug. 3		44 57									33 43		77
10		6.9 39.5						5.0 30			5 30	0.1 0.5	17
20		10 50						5.0 25			5 25		20
30		18.4 91.8						0.2 1			0.8 4.1	0.6 3.1	20
Sept. 4		9 90						1 10					10
Oct. 7		4.2 84						0.6 12			0.2 4		5
Totals	208.3 28.4	320.9 43.7	0.7 0.1	7.1 1.0	31.5 4.3	35.3 4.8	2.0 0.3	50.2 6.8	1.5 0.2	7.8 1.1	55.5 7.6	13.2 1.8	734

TABLE 3.4 Colony H 1964

	Acer pseudoplatanus	Cruciferae	Sarothamnus scoparius	Ranunculus spp.	Trifolium repens	Umbelliferae	Compositae	Chamaenerion angustifolium	Ericaceae	Unknowns	Totals
May 18	150.0 100										150
22	54.5 99.1									0.5 0.9	55
27	82.0 100										82
June 1	24.5 94.2	1.5 5.8									26
10	207.0 100										207
19	78.5 92.4	4.0 4.7								2.5 2.9	85
24		6.5 65	1.5 15	0.1 1			0.7 7	1.2 12			10
July 4		21.3 82			4.2 16	0.3 1	0.3 1				26
13					13.5 80			1.0 6	2.5 14		17
20		12.6 63.0			6.6 33.0		0.2 1.0	0.6 3.0			20
27		5.5 22			11.2 44.9	0.3 1	0.3 1	7.5 30.1		0.3 1	25
Aug. 10		18.9 45			1.7 4			20.6 49	0.8 2		42
20		6.3 42			2.4 16		0.2 1	5.3 35	0.9 6		15
30											0
Totals	596.5 78.5	76.6 10.1	1.5 0.2	0.1 0.0	39.6 5.2	0.5 0.1	1.6 0.2	36.2 4.8	4.2 0.6	3.3 0.4	760

TABLE 3.5 Colony A 1965

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus spp.	Trifolium repens	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Hedera helix	Unknowns	Totals
May 13	162.2 97.8		1.6 1								2.2 1.3	166
14	64.3 96		0.7 1			2.0 3						67
15	0.7 17		3.3 83									4
18	6.4 66.5		3.1 33.5									9.5
19	0.5 32		0.9 62								0.1 6	1.5
23	67.2 85		11.8 15									79
26	33.0 100											33
31	62.0 100											62
June 3	40.5 100											40.5
7	7.0 100											7
11	79.5 100											79.5
14	28.0 95	1.9 4		0.2 0.5		0.2 0.5						29.5
22	14.5 50			14.5 50								29
28		3.6 14.5		17.4 69.5	4.0 16							25
29		3.6 15		7.2 30	12.7 53			0.5 2				24
July 5		0.2 19		0.6 55	0.0 4		0.1 7	0.2 15				1
8		2.7 11.5		17.9 76	0.1 0.2			2.9 12.3				23.5
13		23.8 82		5.2 18								29
19		11.4 35		9.1 28	8.0 24.5	0.3 1		3.7 11.5				32.5
21		10.3 50			10.3 50							20.5

Colony A 1965

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus spp.	Trifolium repens	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Hedera helix	Unknowns	Totals
July 27		3.3 60.5		0.1 1.0	0.4 8	0.03 0.5	0.1 2	1.5 28				5.5
Aug. 2		3.4 82			0.3 6.5		0.4 10	0.1 1.5				4
8		7.3 91.5					0.5 6.5	0.2 2				8
9		1.1 73			0.1 8		0.1 9	0.1 7			0.1 3	1.5
10					1.8 17		8.1 77		0.1 1		0.5 5	10.5
11		2.0 6			1.0 3.5		30 90.5					33
15		15.3 25			15.3 25		30.5 50					61
16		2.3 33			0.1 1.6		4.4 63	0.1 0.7		0.1 0.7	0.1 1	7
17		10.4 47.3		0.1 0.5	3.2 14.5		4.4 20		3.9 17.7			22
19		1.2 39			0.2 6		0.8 26		0.8 28		0.0 1	3
22							1.6 20		6.4 80			8
23		0.3 6					0.3 5.5		4.3 86.5		0.1 2	5
29		0.4 11.7					0.7 23		1.8 58.7		0.2 6.6	3
Sept. 1		0.2 2.6				0.04 0.6	6.6 87.7		0.7 9.1			7.5
6		0.0 1					3.3 82		0.4 9		0.3 8	4
21							20.8 99				0.2 1	21
Oct. 4		3.0 100										3
Totals	565.8 58.3	106.8 11.0	21.4 2.2	72.1 7.4	57.4 5.9	2.6 0.3	112.7 11.6	9.2 0.9	18.3 1.9	0.1 0.0	3.7 0.4	970

TABLE 3.6 Colony H 1965

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Sarothamnus scoparius	Papaveraceae	Ranunculus spp.	Trifolium repens	Compositae	Plantago spp.	Chamaenerion angustifolium	Filipendula ulmaria	Tilia vulgaris	Ericaceae	Unknowns	Totals
May 13	115.3 99							1.2 1							116.5
14	51.8 99.7							0.2 0.3							52
15	1.8 23		6.2 77												8
18	13.4 62.3		8.0 37					0.2 0.7							21.5
19	2.3 28		5.7 71.3					0.1 0.7							8
23	78 95		4 5												82
26	41 95		2 5												43
31	68.5 100														68.5
June 3	62 100														62
7	25 100														25
11	94.3 99.8								0.3 0.2						94.5
14	80 100														80
22	45.8 92.5	1.5 3			0.3 0.5		0.7 1.5						0.3 0.5	1.0 2	49.5
28		2.9 11.5		0.8 3		17.1 68.5	4.1 16.5							0.1 0.5	25
29		3.6 15				8.4 35	11.5 48				0.5 2				24
July 3		3.8 13				6.5 22	14.5 49				3.8 13			0.9 3	29.5
5		4.7 63				0.8 11	0.3 4				1.7 21			0.1 1	7.5
8		9.1 28				8.5 26					11.7 36			3.2 10	32.5
13		25.2 72				4.2 12	1.9 5.5	3.3 9.5						0.4 1	35
19		49.3 46.5				8.0 7.5	47.2 44.5	0.5 0.5						1.1 1	106

Colony H 1965

	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Sarothamnus scoparius	Papaveraceae	Ranunculus spp.	Trifolium repens	Compositae	Plantago spp.	Chamaenerion angustifolium	Filipendula ulmaria	Tilia vulgaris	Ericaceae	Unknowns	Totals
July 21		7.0 19.5				0.2 0.5	27.4 76							1.4 4	36
27						3.0 13	13.2 56			7.3 31					23.5
Aug. 2		0.9 3.5					14.3 54	0.1 0.5		5.6 21	4.5 17	0.9 3.5		0.1 0.5	26.5
8		17.4 54.5					3.2 10			2.2 7	9.1 28.5				32
9		2.9 71					0.8 19			0.3 7	0.1 3				4
10		2.1 17					4.6 36.5			5.7 45.5	0.1 0.5			0.1 0.5	12.5
11		4.3 10.5					4.1 10	0.2 0.5		31.6 78	0.4 1				40.5
15		18.0 14					32 25			71.6 56		1.3 1	3.2 2.5	1.9 1.5	128
16		3.8 25.5				0.2 1	3.1 20.5	0.1 0.5		7.8 52		0.1 0.5			15
17		27.3 52					6.3 12	0.5 1		9.5 18			8.9 17		52.5
19		6.8 54.3					1.5 11.6			1.8 14.6	1.0 7.7		1.4 10.8	1.1 1	12.5
22		0.8 14.5					1.1 20			0.5 8.5			3.1 57		5.5
23		2.2 29.5					0.6 7.5			1.2 16.5			3.5 46.5		7.5
29		1 13					0.7 9.5			5.1 68			0.7 9.5		7.5
Sept. 1		0.1 2.6					1.7 49.3			1.7 48.1				0.0 0.3	3.5
6		0.0 2								2.0 98					2
21										3 100					3
Totals	679.2 49.1	194.8 14.1	25.8 1.9	0.8 0.1	0.3 0.0	56.8 4.1	194.6 14.1	6.3 0.5	0.3 0.0	156.8 11.3	32.8 2.4	2.3 0.2	21.1 1.5	10.4 0.8	1382

APPENDIX 4

Pollen collections from traps 1969 - 16 colonies of honeybees

Note:

1. All weights (g) in the upper part of each box are fresh weights.
2. All percentages are in the lower part of each box.
3. All figures are rounded off to the first decimal place.
4. The order in which the species are arranged is mainly that in which they were collected although variations occur due to the behaviour of the honeybee and other factors.

TABLE 4.1 Colony 9 Pollen collection (1969)

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Betula spp.	Rubus spp.	Sarothamnus scoparius	Crataegus monogyna	Ranunculus spp.	Trifolium repens	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 26	26.1g 30	19.1 22	15.7 18	26.1 30									87
June 3	101.3 34		196.7 66										298
9	300.0 80		75.0 20										375
11	168.0 100												168
18					133.9 66		58.8 29	10.2 5					203
25		15.8 14			63.3 56	33.9 30							113
July 3					12.0 20			3.0 5	45.0 75				60
9		0.4 1			0.4 1			21.8 56	16.4 42				39
18		41.0 24						13.7 8	116.3 68				171
25		205.6 80							17.9 7	12.8 5	20.6 8		257
Aug. 7									146.8 48	116.3 38	42.8 14		306
15									44.5 50	418 47		2.7 3	89
22									65.3 92			5.7 8	71
Sept. 2													0
17													0
22													0
Totals	595.4 26.6	281.9 12.6	287.3 12.8	26.1 1.2	209.6 9.4	33.9 1.5	58.8 2.6	48.7 2.2	452.4 20.2	170.9 7.6	63.4 2.8	8.4 0.4	2237

TABLE 4.2 Colony 38

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus ficaria	Rubus spp.	Sarothamnus scoparius	Crataegus monogyna	Lotus corniculatus	Ranunculus spp.	Trifolium repens	Pinus spp.	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Unknowns	Totals
May 26	88.0 50	19.4 11	29.9 17	38.7 22													176
June 3	357.2 78		100.8 22														458
9	507.0 100																507
11	182.4 95							9.6 5									192
18	369.6 96							15.4 4									385
25					18.7 17	1.1 1	90.2 82										110
July 3		0.9 1							35.3 38	11.2 12					45.6 49		93
9		1.5 6							13.5 54		9.5 38					0.5 2	25
18		120.6 60							13.4 7	67.0 33							201
25									3.0 1	33.0 11		9.0 3	90.0 30	165.0 55			300
Aug. 7													78.9 68	25.5 22		11.6 10	116
15										48.5 50		4.9 5	32.0 33		11.6 12		97
22										57.0 60			9.5 10		28.5 30		95
Sept. 2										10.8 5			183.6 85		21.6 10		216
17									7.4 10	48.1 65			18.5 25				74
Totals	1504.2 49.4	142.4 4.7	130.7 4.3	38.7 1.3	18.7 0.6	1.1 0	90.2 3.0	25 0.8	72.6 2.4	275.6 9.1	9.5 0.3	13.9 0.5	412.5 13.6	190.5 6.3	107.3 3.5	12.1 0.4	3045

TABLE 4.3 Colony 39

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus ficaria	Rubus spp.	Crataegus monogyna	Ranunculus spp.	Trifolium repens	Vicia spp.	Pinus spp.	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 26	0.3 1		23.3 93	1.5 6										25
June 3	50.7 67	25.3 33												76
9	425 100													425
11	58 62				36.0 38									94
18	5 17				75.0 83									80
25					64.0 94	4 6								68
July 3							9.6 12	40 50	11.2 14	8 10			11.2 14	80
9		12.3 25					24.5 50	12.3 25						49
18		125.3 67					3.7 2	50.5 27	7.5 4.0					187
25		100.7 38						79.5 30			39.8 15	45.1 17		265
Aug. 7								41 27			101.8 67	9.1 6		152
15								106.3 85			12.5 10		6.3 5	125
22								47.3 57			4.2 5		31.5 38	83
Sept. 2											27.3 25		81.8 75	109
17											78.9 95		4.2 5	83
Totals	538.9 28.4	263.6 13.9	23.3 1.2	1.5 0.1	175 9.2	4 0.2	37.8 2.0	376.8 19.8	18.7 1.0	8 0.4	264.3 13.9	54.2 2.9	134.9 7.1	1901

TABLE 4.4 Colony 11

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus ficaria	Rubus spp.	Crataegus monogyna	Ranunculus spp.	Trifolium repens	Vicia spp.	Compositae	Sambucus nigra	Scabious	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 26	128 64	4 2	42 21	26 13												200
June 3	174 31	11 2	375 67													560
9	486 92		42 8													528
11	95 59				65 41											160
18	13 5				243 95											256
25		4 4			79 89	6 7										89
July 3		6.6 7			14.1 15		28.2 30	34.8 37			10.3 11					94
9		70.0 62					32.8 29	10.2 9								113
18		182.8 74					29.6 12	12.4 5	22.2 9							247
25		173.9 51						136.4 40					6.8 2	23.9 7		341
Aug. 7								76.8 38		2.0 1			115.1 57	8.1 4		202
15								117.9 88					16.1 12			134
22								68.8 62					5.6 5		36.6 33	111
Sept. 2													19 76		6 24	25
17								1.3 5				1 4	17.2 66		6.5 25	26
Totals	896.0 29	452.3 14.7	459.0 14.9	26.0 0.8	401.1 13.0	6.0 0.2	90.6 2.9	458.5 14.9	22.2 0.7	2.0 0.1	10.3 0.3	1.0 0.0	179.6 5.8	31.6 1.0	49.1 1.6	3086

TABLE 4.5 Colony 50

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Rubus spp.	Sarothamnus scoparius	Ranunculus spp.	Trifolium repens	Compositae	Plantago spp.	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Unknowns	Totals
May 26	180 59	9.2 3	115.9 38											305
29	116.9 37		199.1 63											316
June 3	138.2 51		132.8 49											271
6	264 100													264
9	458.8 97												14.2 3	473
13	356 100													356
18		24.9 11		169.5 75	31.6 14									226
25		60.1 39		87.8 57		6.2 4								154
July 3		97.9 48				26.5 13	51 25						28.6 14	204
7		2.3 6				29.6 76	5.5 14		1.6 4					39
16		29.8 12				67 27	141.4 57	5 2			5 2			248
25		6.2 7					79.2 89			3.6 4				89
Aug. 5							70.6 83			12.8 15	1.7 2			85
8							33.6 58			23.2 40	1.2 2			58
15		13.5 7					125.5 65			27 14		27 14		193
20		0.7 1					3.4 5			2.7 4		61.2 90		68
Sept. 2										0.4 1		42.6 99		43
18										1.3 6		19.7 94		21
Totals	1513.9 44.4	244.5 7.2	447.8 13.1	257.3 7.5	31.6 0.9	129.3 3.8	510.1 14.9	5 0.2	1.6 0.1	70.9 2.1	7.8 0.2	150.5 4.4	42.8 1.3	3413

TABLE 4.6 Colony 32

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ranunculus ficaria	Prunus spp.	Rubus spp.	Ranunculus	Trifolium repens	Compositae	Chamaenerion angustifolium	Ericaceae	Totals
May 26	30.6 12		155.6 61	40.8 16					28.1 11			255
29	87.8 48		95.2 52									183
June 3	106.5 71		43.5 29									150
6	95 100											95
9	270.5 98	5.5 2										276
13	106.7 84				6.4 5	14.0 11						127
18		14.4 14				88.6 86						103
23		21.9 43				16.8 33						51
July 3		56.2 72				6.2 8	15.6 20					78
7		2.5 10					22.5 90					25
16		25.5 25					61.2 60	15.3 15				102
25		19.1 33						24.4 42	1.7 3	12.8 22		58
Aug. 5		0.8 2						8.7 23		28.5 75		38
8								5.3 12		38.7 88		44
15								50 63		5.5 7	23.7 30	79
20								16.8 28		16.8 28	26.4 44	60
Sept. 2								0.7 1		49.7 70	20.6 29	71
18								1.2 2		47.2 80	10.6 18	59
Totals	697.1 37.6	145.9 7.9	294.2 15.9	40.8 2.2	6.4 0.3	125.6 6.8	99.3 5.4	122.1 6.6	29.8 1.6	199.2 10.7	81.3 4.4	1854

TABLE 4.7 Colony 25

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Rubus spp.	Sarothamnus scoparius	Sambucus nigra	Ranunculus spp.	Trifolium repens	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Ericaceae	Totals
May 26	88.9 57		35.9 23						31.2 20				156
29	198.2 84		33 14						4.7 2				236
June 3	276.9 71		113.1 29										390
6	289 100												289
9	524 100												524
13	259.8 68	19.1 5			103.1 27								382
18		10.4 5		147 71	49.7 24								207
23		34.8 29		85.2 71									120
July 3		113.6 71		19.2 12			14.4 9	9.6 6					160
7		5.9 12					38.7 79	3.4 7					49
16		61.6 16				65.5 17	46.2 12	211.8 55					385
25		10.7 4						195.6 73		59 22	2.7 1		268
Aug. 5		9.1 5						124.9 69		41.6 23	5.4 3		181
8		30.5 25						69.5 57		22 18			122
15		68.6 27						101.6 40		78.7 31		5.1 2	254
20		1.4 2						16.6 24		4.8 7		46.2 67	69
Sept. 2										17.3 36		30.7 64	48
18										60.8 79		16.2 21	77
Totals	1636.8 41.8	365.6 9.3	182 4.7	251.4 6.4	152.8 3.9	65.5 1.7	99.3 2.5	733 18.7	35.2 0.9	284.2 7.2	8.1 0.2	98.2 2.5	3917

TABLE 4.8 Colony 28

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Ulex europaeus	Rubus spp.	Sarothamnus scoparius	Lotus spp.	Allium ursinum	Ranunculus spp.	Trifolium repens	Umbelliferae	Sambucus nigra	Compositae	Chamaenerion angustifolium	Ericaceae	Totals
May 26	126.8 31		175.9 43	69.5 17									36.8 9			409
29	123.9 22		349.1 62	67.6 12									22.5 4			563
June 3	476 68		224 32													700
6					537 98							11 2				548
9	783 100															783
13	395.2 76	26 5			72.8 14			26.0 5								520
18		25.4 10			177.8 70	50.8 20										254
23		36.8 10			257.6 70	73.6 20										368
July 3		262.4 80			13.1 4		6.6 2		26.2 8	19.7 6						328
7		61 54							52 46							113
16		387 50							356 46		31 4					774
25		186 35								191.5 36			42.6 8	111.7 21		532
Aug. 5										300.8 75	4 1		12 3	84.2 21		401
8										160.4 79				42.6 21		203
15										73.3 37			6 3	65.3 33	53.5 27	198
20		1.5 2								22.8 30				27.4 36	24.3 32	76
Sept. 2														7.8 25	23.3 75	31
18														16 80	4 20	20
Totals	1904.9 27.9	986.3 14.5	748.9 11	137.1 2	1058.4 15.5	124.4 1.8	6.6 0	26.0 0.4	434.3 6.4	768.4 11.2	35 0.5	11 0.2	119.9 1.8	355 5.2	105 1.5	6821

TABLE 4.9 Colony 13

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Aesculus hippocastanum	Rubus spp.	Crataegus monogyna	Lotus spp.	Echium vulgare	Papaver spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Campanula spp.	Sambucus nigra	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Totals
May 26	260 80	65 20																	325
June 3	390 75	126 24		5 1															521
5	137 99	1 1																	138
8	493 85		58 10		23 4	6 1													580
12	86.4 20		86.4 20		86.4 20	86.4 20				86.4 20									432
18	58.0 20		217.5 75	14.5 5															290
23			14.3 10	7.1 5		21.6 85													143
July 2		55.1 37					6 4	26.8 18	40.2 27										149
8		18.3 25					5.1 7		49.6 68										73
17		25.5 25						3.1 3	40.8 40		9.2 9		2 2	18.4 18		3.1 3			102
25							3.4 3		39.6 35		30.5 27				3.4 3	4.5 4	31.6 28		113
30									19.5 39			6.5 13			2.5 5		21.5 43		50
Aug. 5									17 20		13.6 16						49.3 58		85
14									28.1 26								73.4 68	6.5 6	108
21		1 9							0.3 3								9.7 88		11
Totals	1424.4 45.7	291.9 9.4	376.2 12.1	26.6 0.9	109.4 3.5	214.0 6.9	14.5 0.5	29.9 1	235.1 7.5	86.4 2.8	53.3 1.7	6.5 0.2	2 0.1	18.4 0.6	5.9 0.2	7.6 0.2	185.6 6.0	6.5 0.2	3120

TABLE 4.10 Colony 27

Date	Acer pseudoplatanus	Cruciferae	Viola spp.	Prunus spp.	Rubus spp.	Crataegus monogyna	Lotus spp.	Echium vulgare	Papaver spp.	Trifolium repens	Vicia spp.	Umbelliferae	Compositae	Scabiosa	Chamaenerion angustifolium	Unknowns	Totals
May 26	112 90	1 1	8.5 7										2.5 2				124
June 3	2627 85	46.4 15															309
5	99 100																99
8	362 82			57 13												22 5	441
12	196.4 85				32.3 14					2.3 1							231
18					19.8 33	26.4 44											60
23		9.8 39			3.8 15	4.3 17	5.3 21									2 8	25
July 2		27 37						20.4 28	25.6 35								73
8		36.6 53						4.1 6	17.3 25			4.8 7	0.7 1			1.4 2	69
17					38 52			9.5 13		6.6 9		6.6 9		11.7 16	0.7 1		73
25					8.4 19			3.1 7	6.2 14	8.8 20		8.8 20			8.8 20		44
30					2.5 13			2.5 13	2.5 13		0.6 3	0.8 4		0.2 1	10.1 53		19
Aug. 5								12.4 27	9.7 21	4.6 10		4.6 10			14.7 32		46
14								2.1 5	12.6 30	4.2 10		2.1 5			21 50		42
21		3.6 13								5.4 20					18 67		27
Totals	10321 61.4	124.3 7.4	8.5 0.5	57 3.4	104.6 6.2	30.7 1.8	5.3 0.3	54.1 3.2	73.7 4.4	31.9 1.9	0.6 0	27.7 1.6	3.2 0.2	11.9 0.7	73.3 4.4	25.4 1.5	1682

TABLE 4.11 Colony 56

Date	*Acer pseudoplatanus*	Cruciferae	*Fagus sylvatica*	*Rubus* spp.	*Crataegus monogyna*	*Lotus* spp.	*Echium vulgare*	*Papaver* spp.	*Trifolium repens*	Umbelliferae	*Sambucus nigra*	Compositae	*Chamaenerion angustifolium*	Totals
May 26	190 85	29 13										4 2		223
June 3	351.5 95	18.5 5												370
5	79 100													79
8	243 82		6 2		47 16									296
12	54.3 27				142.7 71				4 2					201
18	43.8 22				155.2 78									199
25			0.3 1	12.1 39	18 58			0.6 2						31
July 4		32 35				4.5 5	18 20	32 35				4.5 5		91
9		27.5 50						22 40		2.8 5	2.8 5			55
17		12 20		9 15			3 5	28 45	3 5	6 10				61
25		2 5		5 10				9 20	7 15	5 10		2 5	15 35	45
30				2 5			3 10	13 40	0	2 5			13 40	33
Aug. 5									24.1 65				13 35	37
14									26.5 50				26.5 50	53
22		0.5 5							5 55				3.6 40	9
Totals	961.6 53.9	121.5 6.8	6.3 0.4	28.1 1.6	362.9 20.4	4.5 0.3	24 1.4	104.6 5.9	69.5 3.9	15.8 0.9	2.8 0.2	10.5 0.6	71.1 4	1783

TABLE 4.12 Colony 51

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Aesculus hippocastanum	Rubus spp.	Crataegus monogyna	Papaver spp.	Ligustrum vulgare	Trifolium repens	Vicia spp.	Umbelliferae	Sambucus nigra	Melilot spp.	Compositae	Chamaenerion angustifolium	Unknowns	Totals
May 26	264 81	45 14												16 5			325
June 3	400 90	44 10															444
5	146 99		1 1														147
8	296 66				153 34												449
12	300.8 89			6.8 2												30.4 9	338
18	35.5 16					159 72						11 5	15.5 7				221
23		25.7 24				71.7 67								9.6 9			107
July 2							84 73	18.4 16				5.8 5		6.9 6			115
8		7.8 17					32.2 70				5.1 11			0.9 2			46
17		9.9 14					39.1 55		9.9 14		12.1 17						71
25		6.9 7					39.2 40		4.9 5		6.9 7				40.2 41		98
30		3.6 7					34.8 67				4.7 9				8.8 17		52
Aug. 5							58.5 78		5.3 7	2.3 3					9.0 12		75
14							96 80								24 20		120
22							21.3 85								3.8 15		25
Totals	1442.3	142.9	1	6.8	153	230.7	405	18.4	20.1	2.3	28.7	16.8	15.5	33.5	85.8	30.4	2633
	54.8	5.4	0	0.3	5.8	8.8	15.4	0.7	0.8	0.1	1.1	0.6	0.6	1.3	3.3	1.2	

TABLE 4.13 Colony 48

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Aesculus hippocastanum	Rubus spp.	Crataegus monogyna	Lotus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Sambucus nigra	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Totals
May 26	4.7 67	2.3 33													7
28	71 93	4 6	1 1												76
June 3	231 100														231
5	112 90			13 10											125
8	332 90				37 10										369
13					22 4	419 78	48 9				48 9				537
18		47 11				382 89									429
25		45 46			11 11	9 9	9 9	20 21	4 4						98
July 4		20 39					6.3 12	22 42		0.5 1	3 6				52
9		5.5 44						5.5 42				2 14			13
17								251 83				45 15	6 2		302
25		6 3					10 5	69 35	10 5	10 5		32 16	49 25	11 6	197
Aug. 5								27 24				6 5	44 39	37 32	114
14		7.5 5						24.5 16	12.3 8				47.5 31	61.3 40	153
22		39 46						4.3 5				34.9 41	5.1 6	1.7 2	85
Sept. 2		15.4 28										39.6 72			55
17		1 5										19 95			20
Totals	750.7 26.2	193 6.7	1 0	13 0.5	70 2.4	810 28.3	73.3 2.6	423.3 14.8	26.3 0.9	10.5 0.4	51 1.8	178.5 6.2	151.6 5.3	111 3.9	2863

TABLE 4.14 Colony 12

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Crataegus monogyna	Lotus spp.	Echium vulgare	Papaver spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Sambucus nigra	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Totals
May 26	239 88	19 7	8 3										5 2			271
28	140 89	11 7	6 4													157
June 3	440 97		14 3													454
5	145 89											18 11				163
8	275 67	135 33														410
13	82.8 19			274.7 63					78.5 18							436
18		35 14		198 80			2 1		12 5							247
25		175 80		13 6					18 8	13 6						219
July 4		120.5 40			30 10			30 10	120.5 40							301
9		28.8 30			4.8 5			4.8 5	28.8 30	9.6 10			14.4 15		4.8 5	96
17		53.0 15							176.5 50				70.6 20	17.7 5	35.3 10	353
25		7 2							140 39	32 9			25 7	104 29	51 8	359
Aug. 5		104 32			3 1				72 22	3 1			26 8	65 20	52 16	325
14		11.5 7								1.6 1	1.6 1		14.7 9	94.5 58	39.1 24	163
22					1.4 8	0.7 4			0.7 4	1.0 6			2.9 38	3.8 17	6.5 23	17
Sept. 2		2.3 25							1.8 20	0.5 5			4.5 50			9
17					1.3 18					0.9 14			4.8 68			7
Totals	1321.8	702	28	485.7	40.5	0.7	2	34.8	648.8	61.6	1.6	18	167.9	285	188.7	3987
	33.2	17.6	0.7	12.2	1.0	0	0.1	0.9	16.3	1.5	0	0.5	4.2	7.2	4.7	

TABLE 4.15 Colony 30

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Aesculus hippocastanum	Rubus spp.	Crataegus monogyna	Lotus spp.	Papaver spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Sambucus nigra	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Totals
May 26	242 83	32 11	17 6														291
28	156 84	15 8	15 8														186
June 3	365 85		21 5	21 5		21 5											428
5	116 97	3 3															119
8	275 85					49 15											324
13	43.2 10				43.2 10	345.6 80											432
18		31 10				190 62				55 18		31 10					307
25		127 50				26 10				38 15			64 25				255
July 4		116 35							33 10	119 36	13 4		49 15				330
9		4 3					8 7		2	16 14	12 10	4 3	71 61				117
17									14 4	120 33			117 32	106 29	7 2		364
25							30 14	81 37		29 13	29 13	2 1		9 4	11 5	29 13	220
Aug. 5							3.5 5			8.5 12		3.5 5		16.5 23	3.5 5	35.5 50	71
14							8.6 4			2.1 1				14.9 7	8.5 4	178.9 84	213
22										0.8 2				4.4 12		31.8 86	37
Totals	1197.2 32.4	328 8.9	53 1.4	21 0.6	43.2 1.2	631.6 17.1	50.1 1.4	81 2.2	49 1.3	388.4 10.5	54 1.5	40.5 1.1	301 8.2	150.8 4.1	30 0.8	275.2 7.5	3694

TABLE 4.16 Colony 35

Date	Acer pseudoplatanus	Cruciferae	Fagus sylvatica	Crataegus monogyna	Lotus spp.	Papaver spp.	Ranunculus spp.	Trifolium repens	Vicia spp.	Umbelliferae	Compositae	Chamaenerion angustifolium	Filipendula ulmaria	Totals
May 26	116 86	14 10	3 2			3 2								136
28	45 86	5 9	3 5											53
June 3	185 100													185
5	57 100													57
8	213 100													213
13	17 8			189 89				6 3						212
18	12 8			132 89				4 3						148
25		74 97					2 3							76
July 4		76 74			5 5		11 11	5 5	5 5					102
9		5 32					1 7	1 7	4 27		4 27			15
17		23 12						87 46			47 25	9 5	23 12	189
25								38 21	2 1	16 9	27 15	56 31	42 23	181
Aug. 5								8 10		8 10	16 20	23.5 30	23.5 30	79
14								33.3 26	33.3 26		11.5 9	7.7 6	42.2 33	128
22									5.3 25		10.5 50		5.3 25	21
Totals	645 35.9	197 11	6 0.3	321 17.9	5 0.3	3 0.2	14 0.8	182.3 10.2	49.6 2.8	24 1.3	116 6.5	96.2 5.4	136 7.6	1795

APPENDIX 5

The index of diversity

TABLE 5.1

The indices of diversity of pollen collections obtained from colonies of honeybees by pollen traps

Colony	Year	Wt. of pollen harvested (g)	No. of pollen types per collection	Index of diversity	S.e. of index of diversity
X	1963	7709	11	1	± 0.1
Y	1963	1726	17	3	± 0.3
F	1964	691	12	2	± 0.3
H	1964	760	8	1	± 0.3
A	1965	969	9	2	± 0.3
H	1965	1382	13	2	± 0.3

(Pollens occurring in amounts less than 0.1% of the total harvest were discounted).

TABLE 5.2

Indices of diversity of the 1969 pollen collections

Colony	Wt. of pollen harvested (g)	No. of types of pollen	Index of Diversity	S.e of index of diversity
9	2237	12	2	± 0.3
38	3045	16	2	± 0.2
39	1901	14	2	± 0.3
11	3085	14	2	± 0.2
50	3413	13	2	± 0.2
32	1854	11	1	± 0.15
25	3917	12	1	± 0.15
28	6821	15	2	± 0.2
13	3018	19	3	± 0.3
27	1682	17	2	± 0.3
56	1783	13	2	± 0.3
51	2633	16	2	± 0.2
48	2863	14	2	± 0.2
12	3987	16	2	± 0.2
30	3694	16	2	± 0.2
35	1795	14	2	± 0.3

(The only significant differences ($p = 0.05$) were between colonies 50, 28, 32 and 25 on one site; there were no significant differences ($p = 0.05$) between colonies on different sites).

APPENDIX 6

Nectar flows

1. The relationship between honey stored and total colony weight

The relationship between honey in store in the honeybee colonies and the total weight of honeybees, brood (eggs, larvae and pupae), honey, and pollen was examined on seven occasions between the 21st May and the 23rd September 1969 in 24 colonies (see Table 6.1). The mean correlation coefficient was 0.941 which is very highly significant ($p = 0.001$) indicating that a close relationship existed between these two variables. Therefore the total colony weight could be used as an indication of the fluctuations in the amount of honey stored in the colony. An examination of the data showed that in May, August and September the relationship between honey stored and total colony weights was particularly close but in June and July when the colony population of adults and developing young was at its peak, total colony weights were between 1.5 and 1.7 times the weight of the honey stored. Thus total colony weights were shown to be good indicators of the variation in the honey stored within colonies but if exact determinations were required the colony would require to be examined in detail by an internal inspection.

TABLE 6.1

Total weights of honey, pollen, bees and brood in colonies (1969)

Colony	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
19	18,845g	14,620	20,859	19,637	18,036	23,400	30,989
3	11,107	8,083	20,371	25,555	23,569	30,238	36,701
37	13,021	9,370	16,688	20,645	15,924	25,815	32,404
31	12,193	10,755	23,634	26,193	26,167	26,863	29,135
9	9,924	6,037	9,700	18,047	17,544	19,866	16,449
38	11,683	7,027	21,705	19,441	21,668	32,268	36,940
39	11,324	7,702	15,257	21,776	25,482	46,388	56,498
11	5,032	10,138	11,704	19,523	33,436	26,374	34,582
50	7,545	5,744	11,883	14,203	19,394	12,010	12,329
32	10,165	8,455	26,741	27,035	19,055	29,595	35,278
25	9,698	7,331	14,179	20,878	13,738	11,538	15,298
28	13,452	9,874	20,381	28,020	19,834	29,353	24,108
8	3,036	12,209	24,398	22,159	15,219	20,132	14,746
53	14,124	18,046	30,126	27,416	26,396	17,652	15,862
36	15,161	10,273	15,774	10,360	25,095	24,507	26,543
44	10,448	13,501	27,515	22,169	19,094	8,290	5,709
13	9,249	11,632	25,240	28,134	26,009	8,859	7,931
27	11,273	10,505	17,421	24,365	19,156	19,209	16,066
56	10,090	10,217	23,128	27,097	20,441	20,125	15,630

51	12,407	13,359	21,920	25,899	20,809	9,349	6,405
48	18,302	14,696	26,789	28,032	20,043	13,126	11,624
12	4,702	13,524	14,916	18,901	18,945	16,771	16,733
30	13,207	15,371	20,139	20,887	18,848	18,523	14,225
35	13,651	14,386	17,477	17,378	13,892	6,979	3,513
r^1 =	0.942	0.874	0.898	0.937	0.950	0.988	0.998

[1] = correlation coefficient between honey stored and total colony weights on these dates.

TABLE 6.2

The colony weights in kilograms throughout 3 seasons on the six sites

		April	May		June		July		August		Sept.
		30	15	30	15	30	15	30	15	30	15
Coastal Area											
(1) Fettes	1964	6	2	15	27	22	16	19	16	13	10
	1965	3	4	13	14	9	5	5	7	4	2
	1966	5	3	14	17	13	8	10	8	5	3
(2) Dirleton	1964	4	3	13	19	15	11	13	13	11	8
	1965	1	5	17	22	20	18	16	19	22	17
	1966	3	7	18	24	20	17	21	18	16	13
(3) Longniddry	1964	7	3	20	27	19	18	22	18	15	13
	1965	3	9	23	35	29	24	23	23	23	19
	1966	5	5	21	22	15	15	18	15	13	10
Upland Area											
(4) Bush	1964	6	1	20	29	27	26	37	41	57	50
	1965	3	5	17	18	11	7	5	9	18	17
	1966	4	1	11	11	10	9	18	18	32	27
(5) Houndleshope	1964	4	3	16	26	23	23	34	47	53	48
	1965	6	1	23	17	13	14	13	23	22	17
	1966	7	3	7	15	11	19	37	45	44	39
(6) Lauder	1964	7	1	9	4	21	34	42	48	56	60
	1965	5	5	12	9	8	8	10	8	18	19
	1966	8	3	6	0	0	17	38	42	47	48

APPENDIX 7

Colony data 1969

TABLE 7.1

Pollen stored g 1969

Colony	Examination dates						
	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
19	1,050	1,330	4,475	2,560	1,105	1,760	1,255
3	1,135	1,135	3,635	2,375	2,035	3,445	1,905
37	530	910	3,650	2,505	1,705	2,960	830
31	755	1,560	3,730	2,655	2,820	2,780	1,355
9	605	490	3,150	3,010	1,440	1,495	1,045
38	870	655	2,695	1,235	960	2,315	1,685
39	410	620	2,460	1,580	2,620	3,303	835
11	700	540	2,430	980	1,675	3,145	1,465
50	760	970	2,450	2,145	1,285	1,685	1,035
32	1,005	1,610	3,025	2,405	2,130	3,290	1,440
25	665	1,110	1,715	1,550	820	1,410	685
28	1,250	1,425	1,350	1,350	1,360	1,170	610
8	215	845	2,605	1,820	1,860	1,985	720
53	465	1,185	2,498	1,475	955	960	310
36	103	750	1,555	1,650	820	1,135	410
44	800	1,930	4,530	2,735	2,840	1,905	1,655
13	1,860	1,680	3,010	2,815	2,605	1,225	1,190
27	640	1,360	1,790	1,025	1,710	1,360	1,275
56	935	1,200	3,055	1,200	755	1,740	385
51	1,675	2,200	3,325	2,110	2,500	640	235

48	1,680	1,795	4,710	2,650	1,230	1,020	510
12	810	1,725	2,635	1,870	1,875	1,625	1,680
30	2,055	2,455	3,695	2,520	2,475	2,100	2,145
35	1,105	1,475	2,340	1,355	650	325	15
Mean (24)±s.e.	960± 97	1,310±108	2,930±187	1,995±130	1,680±144	1,828±175	1,030±118

TABLE 7.2

Honey stored g 1969

Colony	Examination dates 21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
19	14,742	11,201	14,994	15,322	14,049	17,917	28,224
3	6,111	2,205	12,600	17,527	15,145	23,537	33,528
37	9,967	5,040	9,576	12,713	8,896	19,946	30,240
31	8,959	5,619	15,863	18,976	19,971	21,382	26,346
9	6,892	2,835	3,213	9,841	11,302	16,405	14,515
38	5,821	1,462	6,678	12,058	15,246	27,279	32,785
39	7,648	3,062	7,182	15,611	17,136	39,892	53,222
11	1,059	4,801	4,322	13,091	26,082	20,059	31,374
50	4,952	2,482	6,413	8,492	14,566	8,051	10,798
32	4,801	1,890	17,993	17,854	10,571	21,546	31,802
25	6,098	3,087	8,575	15,208	8,707	7,384	13,847
28	9,727	5,607	15,032	17,967	13,129	20,286	22,478
8	1,058	8,001	17,174	14,515	10,710	15,523	12,297
53	11,403	11,907	23,058	20,638	18,245	14,251	14,099
36	12,802	8,455	13,432	8,379	19,933	20,638	24,456
44	5,418	8,228	18,408	14,263	12,323	4,460	3,125
13	3,793	6,073	17,766	20,349	18,333	6,186	5,720
27	9,223	6,527	12,802	18,711	12,524	16,745	14,175
56	5,456	4,397	14,528	19,366	14,981	15,939	13,608
51	7,673	6,804	14,238	16,959	12,361	7,195	5,002

48	12,348	8,392	16,430	18,232	12,474	9,274	10,307
12	2,885	9,437	9,778	13,948	14,036	13,545	13,784
30	9,677	11,252	13,873	13,973	11,857	14,427	10,848
35	10,937	10,685	12,398	12,298	9,765	5,204	3,465
Mean (24)±s.e.	8,265±630	6,224±668	12,776±1008	15,259±718	14,213±844	16,128±1,651	19,165±2,507

TABLE 7.3

Pollen trapped g 1969

	Examination dates						
Colony	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69	Totals
9	385	543	316	99	894	0	2,237
38	634	699	495	118	809	290	3,045
39	101	519	148	129	812	192	1,901
11	760	688	345	207	1,035	51	3,086
50	892	1,093	380	243	741	64	3,413
32	588	498	154	103	381	130	1,854
25	782	1,195	327	209	1,279	125	3,917
28	1,672	1,851	622	441	2,184	51	6,821
13	846	1,150	433	222	367	0	3,120
27	433	771	85	142	251	0	1,682
56	593	576	230	146	238	0	1,783
51	769	934	328	161	441	0	2,633
48	314	1,031	527	65	851	75	2,863
12	882	1,009	466	397	1,217	16	3,987
30	905	875	562	447	905	0	3,694
35	374	482	224	117	598	0	1,795
Means ± s.e.	683±89	870±90	353±39	203±31	813±121	62±21	
Collection rate/day	53	124	29	14	18	2	

TABLE 7.4

Honeybees 1969

Colony	Examination dates						
	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
19	27,600	22,600	15,000	8,400	15,000	26,100	16,000
3	29,400	26,700	21,000	36,800	40,200	21,900	12,300
37	18,800	18,600	18,900	34,500	34,300	19,500	13,700
31	16,700	20,300	21,900	29,100	27,900	19,200	13,500
9	16,500	10,100	16,500	31,600	34,200	15,600	6,800
38	35,300	26,700	31,800	45,700	39,600	13,500	23,200
39	24,000	23,700	28,500	39,100	32,400	22,200	25,600
11	22,200	23,400	29,800	43,400	61,500	18,900	18,200
50	10,500	10,200	18,000	22,500	21,900	17,900	5,400
32	29,800	27,000	32,200	51,100	44,700	30,000	21,100
25	20,800	14,300	22,800	29,100	28,300	21,000	8,100
28	14,600	12,400	21,300	28,500	33,900	18,000	11,100
8	8,600	15,600	25,200	47,100	28,800	22,500	18,800
53	11,550	19,600	25,800	35,800	54,000	21,000	15,800
36	13,500	(6,300)	(6,600)	(3,600)	25,800	24,600	18,000
44	6,900	16,300	27,000	39,700	30,300	20,700	10,100
13	22,200	21,900	27,900	38,400	34,800	12,900	11,100
27	8,100	12,100	19,000	29,300	29,700	12,000	6,700
56	19,800	22,300	29,250	54,500	48,600	18,300	17,800
51	16,500	21,600	24,900	54,600	48,700	10,500	12,700

48	20,400	21,900	34,500	51,000	51,300	24,100	8,600
12	5,100	12,700	14,800	22,800	28,500	14,400	13,800
30	8,500	10,200	12,900	28,800	34,800	18,300	13,400
35	9,000	11,800	14,400	25,200	25,800	12,900	11,100
Means ± s.e.m.	17,348±	18,348±	23,189±	35,957±	35,625±	19,000±	13,871±
	1,695	1,219	1,346	2,463	2,303	1,003	1,096

(The figures in the brackets were omitted from the mean ± s.e. calculations)
because they were atypical

TABLE 7.5

Brood numbers 1969

Colony	Examination dates						
	21.5.69	4.6.69	11.6.69	23.6.69	7.7.69	20.8.69	23.9.69
19*	5,589	115	115	10,695	16,330	14,375	414
3	12,581	24,863	23,966	24,656	29,256	13,501	1,495
37	8,648	18,584	18,745	24,495	23,575	12,121	805
31	10,258	23,115	22,034	20,493	8,809	10,166	2,093
9	9,890	19,389	19,780	24,886	18,009	5,773	2,875
38	18,975	26,680	25,875	21,137	1,978	15,571	3,657
39	11,500	20,010	22,540	10,741	29,854	12,512	943
11*	13,386	28,750	24,035	15,870	230	15,571	759
50	9,430	14,720	14,835	16,261	16,629	6,831	0
32	17,595	26,864	30,015	22,563	24,380	21,735	1,035
25	11,109	19,780	19,481	15,686	17,480	8,832	230
28	12,305	18,515	22,195	22,632	24,219	6,785	0
8*	10,580	20,976	25,070	16,215	0	9,729	0
53	12,995	34,270	23,897	21,850	24,219	5,543	0
36*	11,040	5,336	1,978	0	21,413	5,129	230
44	3,910	20,056	22,770	16,514	12,443	230	0
13	16,905	20,286	20,631	15,640	20,332	2,852	0
27	7,245	16,376	18,653	21,022	23,805	0	0
56	20,424	27,945	31,027	16,491	2,553	8,303	0
51	16,767	25,760	22,471	19,642	15,962	5,957	0

48	26,082	27,140	26,910	26,726	17,618	6,693	184
12	5,865	12,995	12,420	10,718	4,485	3,013	0
30	7,544	7,912	15,065	18,975	14,099	3,404	0
35	8,510	12,420	15,387	15,295	12,006	2,875	138
Means ± s.e. (20)	12,381± 1,294	20,886± 1,412	21,435± 1,095	19,321± 1,016	16,849± 1,812	7,635± 1,212	674± 239

*The data from these colonies were omitted from the calculation of the means and s.e. because of the fluctuations in brood.

TABLE 7.8

Disposition of the colonies 1969

Colony	Site	Trapped	
9, 38, 39, 11	Penicuik	Yes	
19, 3, 37, 31	Bush	No	INLAND
50, 32, 25, 28	Bush	Yes	
8, 53, 36, 44	Broadwood	No	
13, 27, 56, 51	Broadwood	Yes	COAST
48, 12, 30, 35	Maggie's Waas	Yes	

APPENDIX 8

Weather

TABLE 8.1

The temperatures at Bush House 1963-1965 (Anon, 1963-5)

Month	Means of monthly maximum temperatures (°C)		
	1963	1964	1965
March	8.2	5.1	6.7
April	9.9	10.8	10.7
May	12.3	13.7	13.2
June	15.8	15.5	16.2
July	16.7	17.0	14.5
August	15.6	16.6	16.5
September	14.7	15.9	13.8
October	12.8	11.1	11.9
November	8.1	8.8	5.1
December	5.0	5.2	5.4

TABLE 8.2

The weather in 1969[1]

		Air Temperature Daily Mean	Differences[2]	Sunshine Daily Mean	Rain Total fall	Per cent[3]
May	Site Bush	8.5°C		3.34 hr	106 mm	153
	Penicuik	8.5	- 1.1	3.00	104	149
	Haddington	9.5		3.57	61	115
June	Bush	12.3		7.08	53	87
	Penicuik	12.7	+ 0.1	7.01	43	69
	Haddington	13.3		6.69	45	99
July	Bush	14.7		6.23	33	36
	Penicuik	14.7	+ 0.3	5.71	40	43
	Haddington	15.8		6.15	30	45
August	Bush	14.8		5.95	62	64
	Penicuik	15.0	+ 1.1	5.13	71	74
	Haddington	15.9		5.49	36	49
September	Bush	11.9		3.94	64	77
	Penicuik	11.9	0.0	3.74	55	64
	Haddington	13.0		4.08	49	85

[1]Anon, 1970. [2]Differences from 1931-60 mean where recorded

[3]% of 1916-1950 mean.

APPENDIX 9

Chemical Methods

Nitrogen determination

Nitrogen determinations were carried out on approximately 50 mg samples of pollen by a micro-Kjeldahl method using a Markham still (1942) and employing a modification of the method described by Yuen and Pollard (1953). Dry matter determinations were carried out simultaneously on 1 g samples of the same type of pollen from the same sample (see dry matter method, Experimental material and methods).

The pollen for nitrogen estimation was carefully weighed and added to micro-Kjeldahl flasks along with 1½ ml of A.R. sulphuric acid. The flasks were then carefully heated by a small flame in a fume cupboard for 20 minutes, cooled, and half a Selenium catalyst tablet added (supplied by B.D.H.; each tablet contained 1 g sodium sulphate, anhydrous, and the equivalent of 0.05 g of Selenium). Gentle reheating of the flask was resumed until the solution cleared (after 1½ to 2 hours) and then the heating was increased until the solution turned a clear turquoise colour (after a further 30 minutes). The solution was then cooled. About 5 ml of de-ionised water was added to the flask to dissolve any crystals that had formed, the mixture added to a 25 ml standard flask and made up to the mark with de-ionised water. Aliquots of 5 ml were taken,

pipetted into the inner distillation tube of the Markham still, washed in with 5 ml of de-ionised water. Five ml of 20 per cent sodium hydroxide (to drive off the ammonia) were then added and washed in with de-ionised water. Steam was now passed through the still to aid in driving off the ammonia which was then trapped in a flask containing 10 ml of de-ionised water and 6 drops of Tashiros indicator (Conway and Byrne 1933). The distillation rate was adjusted to about 5 ml per minute. After 5 minutes all the ammonia had been expelled from the still and trapped in the flask which was then removed from the still and titrated with N 140 sulphuric acid. The nitrogen was determined in each sample by calculation. Allowance for error was made by blanks throughout the series of estimation and by performing all determinations in duplicate.

Paper chromatography of the sugars fructose and glucose

Shandon chromatographic tanks (Shandon Scientific Co. Ltd., London) and rolls of chromatographic grade Whatman no. 1 were used. Uni-dimensioned descendingpaper chromatography was carried out using a solvent system of ethyl acetate: pyridine: water: 10 : 4 : 3. Lengths of paper were cut from the rolls, serrated at the bottom edge, to facilitate the even flow of solvents down and off the paper. The sugar solutions were spotted on to the paper 2.5 cm apart by an Agla micropipette along a line which was approximately 8 cm from one end.

At the same time aliquots of standard solutions of fructose and glucose were spotted on the paper at the rate of 12 ml per spot. The chromatograms were placed in air tight containers and irrigated by the solvent at 18° C for about 18 hours. The sugars were prepared from the samples of pollen with a dry matter of about 1 g by macerating, extracting twice with distilled water for 5 minutes and filtering through Whatman No. 1 paper. This extract was heated to 80°C, filtered through a Whatman No. 1 paper and made up to 100 ml in a volumetric flask after the pollen had been tested to determine whether all the sugars had been removed.

After about 18 hours the chromatograms were removed from their containers, dried and developed by the method of Trevelyan et al (1950); once the papers had dried the sugar spots were evaluated by a reflectometer unit consisting of an EEL reflectometer head (Mark III) and EEL Unigalvo. (A similar method was devised by Maurizio 1951, 1961 and Sulser 1954). It was found in practice that an oval mask produced higher readings than the round mask supplied with the reflectometer head. The apparatus was operated by placing the masked head completely over the chromatogram spot and recording the maximum Unigalvo reading. These readings were then plotted on semi-logarithmic paper and the sugar concentrations were evaluated with standards run on the chromatogram at the same time. All chromatograms were performed in quadruplicate to ensure greater accuracy and the mean results reported.

Carbohydrate and 'Lignin' in Pollen

The methods used for examining pollen carbohydrates and 'lignin' were modified from McDonald and Henderson (1964), Wylam (1953) and Harwood (1954).

Reducing Sugars: Pollen samples of approximately 1 g were macerated with de-ionised water and made up to 100 ml in standard flasks. Aliquots of 5 ml were removed and made up to 100 ml and 5 ml samples of the latter were examined for reducing sugars by Somogyi's method (1945), and estimated as glucose.

Total Sugar: Fifteen ml aliquots were removed from the 100 ml flask containing the macerate from the pollen and hydrolysed with sulphuric acid (5 ml 2N sulphuric acid) for 10 minutes, neutralised, made up to 200 ml and 5 ml samples removed for Somogyi estimations, which were expressed as glucose.

Normal sulphuric acid extract ('hemicelluloses'): The residue from the water extract of the reducing sugar extract above, was hydrolysed gently for 1 hour with 30 ml of normal sulphuric acid, filtered through glass-paper and made up to 100 ml. A 25 ml sample was made acid by adding 5.8 ml of 4 N sulphuric acid and then hydrolysed for 4 hours in order to hydrolyse the carbohydrate completely. After cooling and neutralising the volume was made up to 50 ml and 5 ml samples were used to determine the soluble sugars by Somogyi; the results were expressed as glucose.

72% acid extract ('cellulose'): The residue from the normal acid extract was treated with 15 ml of 72% W/W sulphuric acid and hydrolysed for 4 hours at 18 ± 2°C, 350 ml of de-ionised water was added to make the solution normal and it was then boiled for 2 hours under reflux, filtered through an asbestos lined Gooch crucible and washed with de-ionised water. The filtrate was made up to 500 ml, an aliquot (20 ml) was taken, neutralised, made up to 50 ml and a Somogyi estimation carried out on a 5 ml aliquot. The results were expressed as glucose.

Insoluble organic residue ('lignin'): The residue from the above extraction was dried at 100°C, weighed, ignited, and the loss on ignition was designated insoluble organic residue.

The determination of calcium, magnesium, potassium, sodium, manganese and phosphorus

Apparatus: A Unicam SP 90 and anSP 900 were used.

Method: The pollen ash from the ash determination was taken to dryness twice with just enough 6N HCl to cover it. (Care was taken to avoid loss through effervescence when the acid was first added to the ash). The ash was then taken up in 5 ml 1.5N HCl, covered with a watch glass and digested on the water bath for 30 minutes. It was filtered hot through a 9 cm Whatman No. 30 paper into a 100 ml graduated flask, washed with hot water, cooled and diluted to 100 ml. Ten

ml of this solution were diluted to 100 ml in a flask containing 10 ml 0.1% phosphate. (The presence of 100 ppm P as phosphate reduces depression of Ca emission by phosphate derived from plant material to negligible proportions). Mg was measured using atomic absorption while Ca was normally determined by emission spectrophotometry. All the standard and sample solutions were read on the Unicam SP 90 for each element. The concentration in each sample was calculated using graphs drawn from the standard readings. For Ca, the galvo deflections obtained with the standards were plotted against their concentrations. The concentrations in the oven dry samples were then calculated by reading the appropriate percentage from the curve and multiplying by a factor of 1000 divided by the weight of oven dry plant material taken. For Mg, the absorbance obtained with the standards were plotted against their concentrations, where absorbance = log 100 divided by galvanometer deflection. The concentrations in the oven dry samples were again calculated by reading the appropriate percentage from the curve and multiplying by the same factor as for Ca. Sodium and magnesium were estimated in a similar manner to calcium on the SP 90 and SP 900 respectively.

The samples were diluted further by a factor of 10 and the amount of potassium present in them calculated by comparison of the readings on the SP 90 with those obtained from standards.

Phosphorus was determined by digesting the pollen with 60% perchloric acid and measuring the colour complex produced on the formation of the phosphovanadomolybdate complex (Hanson 1950).

Nucleic acid estimation

This was carried out on the pollens using a modification of Burton's method (1956), to discover whether they were present in quantities that might be interfering with the calculation of crude protein from the Kjeldahl method for nitrogen.

Method: Pellets of the various pollen types were weighed carefully, their dry matter was determined and they were then incubated in duplicate with 5% perchloric acid for 20 minutes at 70°C. The solutions were centrifuged, the clear fluid was decanted off and mixed with diphenylamine reagent and incubated overnight at 34°C. Standard solutions of deoxyadenosine were also prepared for comparison with the pollen solutions; these were performed on a Unican SP 500 and read at wavelengths of 260 and 280 microns.

Amino acid determination

Apparatus: A Technicon amino acid auto analyser (as supplied by Technicon Instruments Ltd., Chertsey, Surrey, England).

Procedure for operating the auto analyser: The procedure was that described by Waring and Bolton (1967) using single columns and a modified Thomson and Miles (1964) buffer system. The colour reagent was 2 : 4 : 6 trinitro-benzene sulphonic acid. The pumping rate was adjusted to 0.9 ml/min. so that each chromatogram took about 10 hours to complete. Zeocarb 224 (8% cross linking; average particle size 21 microns) was used as the cationic exchange resin.

Method: The sample was prepared for analysis by being ground as finely as possible and a sub-sample containing between 16 and 24 mg of nitrogen was weighed out and placed in a two-necked 1 litre round bottom flask. 800 mls of oxygen free hydrochloric acid were added to the flask and shaken to disperse the acid. A reflex condenser was fitted, the apparatus was flushed out with nitrogen and heating commenced. The sample was heated to boiling for 20 hours under a continuous stream of nitrogen on an iso-mantle. The sample was then cooled in a stream of nitrogen and when cool 20 mls of norleucine standard added. (Nor-leucine standard: 0.2624 g of norleucine in 500 ml N/10 HCl). The condenser contents were washed down into the flask, made up to 1 litre, mixed thoroughly, and filtered (Whatman No. 540 filter paper). About 125 ml of filtrate was collected and evaporated to dryness at 40°C on a rotary evaporator. When it was dry 2.5 ml of N hydrochloric acid was added to dissolve the residue which was then

made up to 25 ml. A portion of the hydrolysate was transferred to a plastic bottle and stored in a deep freeze until analysed. Amino acid analysis was performed on 1.0 ml of the solution, representing 1/200th of the total sample. The 1.0 ml sample was applied to the top of the appropriate ion exchange column of the automatic amino acid analyser. The effluent from the column was pumped through a heating coil to develop the colour which was recorded as peaks on a logarithmic chart. The peaks were integrated by a process of triangulation.

Accuracy of method: The accuracy of the analytical technique used was examined by analysing 12 samples from a standard mixture containing known amounts of each of the amino acids determined (Waring and Bolton, 1967). Norleucine was used as an internal standard and the amount of each of the amino acids was calculated from the amount of internal standard added to the standard mixture and the relative colour development of each amino acid relative to the norleucine. The mean colour factors and their standard errors relative to norleucine = 1.00 are presented in the Table on the following page.

From the data presented (Table 9.1) it is obvious from the statistical calculations that the accuracy of the determination of the various amino acids is very high.

TABLE 9.1

Reproducability of Amino Acid Analytical Method

Amino Acid	Mean Colour Factor	Standard Error
Aspartic acid	1.49	± 0.02
Threonine	0.86	± 0.01
Serine	0.96	± 0.01
Glutamic acid	1.31	± 0.02
Glycine	0.96	± 0.01
Alanine	1.21	± 0.01
Valine	0.83	± 0.00
Cystine	0.59	± 0.01
Methionine	0.95	± 0.01
Isoluecine	0.86	± 0.01
Leucine	1.04	- -
Tyrosine	1.07	± 0.01
Phenylalanine	1.00	± 0.01
Ornithine	0.56	± 0.01
Lysine	0.58	± 0.01
Histidine	1.07	± 0.01
Arginine	0.85	± 0.01

(Colour factors are reciprocals of peak area/micromole relative to norleucine = 1.00 and leucine = 1.04).

The determination of sodium, calcium, potassium, and magnesium in honey

Sampling: Over 90 samples of honey were collected during three seasons. The honey which originated from the North of the United Kingdom was predominantly from the East of Scotland. No attempt was made to class the honey into different floral types as most of the samples were of mixed floral origins and pure samples of honey are seldom obtained in Britain.

Analytical methods: The samples were heated for 3 hours at 80°C. When the honey had softened sufficiently the wax was skimmed off the surface. The sample was then diluted 40-fold with distilled water for the determination of Na, Mg and Ca. For the estimation of K the honey had to be diluted from 100 to 500 times dependent on the concentration.

Na, Ca and K were determined by the use of flame-photometric methods while Mg was estimated by atomic absorption. The instrument used was, in both cases, a Unicam SP 900 A. Diluted samples were fed directly into the Unicam. The accuracy of this procedure was checked by taking several samples of the honey which were ashed and extracted before being fed into the instrument. This second method was more tedious and no more accurate in the determination of the cations.

Although it is usual to express the results of the analysis of plant material as a percentage of their dry matter, this is not convenient, when working withhoney. The results are all expressed as parts per million weight/volume.

APPENDIX 10

Results of chemical analyses

TABLE 10.1

Percentage dry matter of pollen trapped in 1969 a.

Site	Colony	May		June					
		25th	29th	3rd	6th	8th	11th	18th	25th
Penicuik									
	9	78.27		78.07		75.17	75.69	69.88	72.45
	38	68.98		76.63		71.02	72.41	68.94	75.24
	39	76.68		76.34		71.33	72.10	72.43	73.24
	11	73.65		73.39		72.73	76.86	70.06	73.21
Bush									
	50	69.92	78.80	75.49	77.70	74.63	77.31	77.09	77.87
	32	73.30	73.49	71.86	77.73	70.38	77.22	71.65	75.91
	25	77.07	75.84	73.41	71.80	74.80	76.38	71.72	72.24
	28	71.60	73.66	73.47	73.98	73.20	76.62	71.60	74.20
Broadwood									
	13	74.94		62.87	75.80	73.25	74.59	70.22	74.53
	27	80.26		67.23	81.52	70.19	76.57	76.74	72.46
	56	69.97		67.76	69.51	74.34	73.94	72.66	81.67
	51	74.97		70.72	68.74	74.99	76.31	69.90	79.32

Maggie's Waas	48	N.P.	76.32	69.14	70.75	68.96	73.53	70.17	76.26
	12	68.00	74.38	71.55	71.55	71.93	76.10	71.48	78.19
	30	67.77	77.39	67.53	75.91	70.73	73.48	72.37	73.09
	35	71.75	71.23	66.53	74.62	70.41	74.12	70.59	76.17

(N.P. signifies no pollen had been collected from the bees).

TABLE 10.2

Percentage dry matter in pollen trapped in 1969 b.

Site	Colony	July 3rd	8th	18th	25th	30th	August 6th	8th	15th	21st	September 2nd	18th	22nd
Penicuik													
	9	74.06	79.30	77.04	70.57		68.62		67.60	84.12	N.P.	N.P.	N.P.
	38	76.36	81.59	78.13	67.23		70.86		64.06	75.98	59.20	78.48	N.P.
	39	75.35	76.00	76.83	69.72		72.34		68.39	85.59	58.97	78.19	N.P.
	11	77.59	76.04	78.01	71.59		70.49		68.90	76.57	73.61	80.46	N.P.
Bush													
	50	75.02	79.53	76.10	79.18		69.97		61.75	73.46	66.07	66.96	N.P.
	32	76.22	77.86	78.41	78.66		71.31		71.14	73.85	66.17	62.02	N.P.
	25	75.58	75.79	73.04	71.91		72.48		62.64	76.79	63.48	55.45	N.P.
	28	74.93	74.84	75.36	73.75		69.76	72.03	66.19	76.33	66.08	65.21	N.P.
Broadwood													
	13	70.76	71.72	75.58	67.01	79.86	75.29	73.03	67.02	80.66	N.P.	N.P.	N.P.
	27	75.47	73.01	77.09	73.90	79.92	74.87	76.41	78.28	78.36	N.P.	N.P.	N.P.
	56	75.09	74.77	76.37	70.13	79.97	77.86	71.00	80.83	82.28	N.P.	N.P.	N.P.
	51	76.27	72.63	76.11	69.12	80.58	73.40		72.61	79.69	N.P.	N.P.	N.P.

Maggie's Waas										
48	75.55	78.52	71.58	65.30	72.10	71.22	70.03	66.48	73.17	N.P.
12	76.28	75.72	75.01	66.50	67.29	71.20	79.24	69.99	77.66	N.P.
30	53.92	79.59	70.27	65.64	71.63	66.34	72.52	N.P.	N.P.	N.P.
35	73.23	81.21	69.72	66.32	84.08	73.89	72.67	N.P.	N.P.	N.P.

(N.P. signifies no pollen had been collected from the bees).

TABLE 10.3

The ether extract of pollens (as % dry matter)

	Samples				
Pollen type	1	2	3	4	mean
Beech	16.4	9.1	9.4	12.4	11.8
Buttercups	2.2	2.5	2.4	2.2	2.3
Crucifers	8.1	7.6	7.9	7.7	7.8
Heaths	2.0	1.4	1.8	1.7	1.7
Rosebay willow-herb	2.2	1.7	1.9	2.1	2.0
Sycamore	4.0	3.2	3.9	3.4	3.6
White clover	2.4	3.0	2.7	2.8	2.7

TABLE 10.4

The ash of pollens (as % dry matter)

	Samples				
Pollen type	1	2	3	4	mean
Beech	2.36	1.75	1.91	1.79	1.95
Buttercups	2.80	2.90	2.82	2.89	2.85
Crucifers	3.22	4.24	3.76	4.14	3.84
Heaths	2.54	2.94	2.88	2.67	2.76
Rosebay willow-herb	2.90	2.70	2.79	2.83	2.81
Sycamore	3.28	3.45	3.33	3.49	3.39
White clover	3.00	3.45	3.27	3.42	3.29

TABLE 10.5

The nitrogen content of pollen (as % dry matter)

	Samples								
	1	2	3	4	5	6	7	means	S.e. of difference between pollen means
Beech	2.31	2.47	2.57	2.95	2.44	2.77	2.53	2.58	
Buttercups	3.08	3.11	3.76	2.37	3.21	3.09	2.96	3.08	
Crucifers	4.99	5.20	5.12	4.38	5.03	4.64	5.71	5.01	
Heaths	3.55	3.11	3.44	3.61	3.58	3.77	3.92	3.57	± 0.19
Rosebay willow-herb	3.29	3.76	3.78	2.96	3.60	3.73	3.54	3.52	
Sycamore	5.61	5.58	4.95	5.06	6.19	5.96	5.46	5.54	
White clover	4.06	4.63	4.25	5.40	4.96	4.81	4.64	4.68	

TABLE 10.6

Pollen glucose (as % dry matter)

	Samples				
Pollen types	(1)	(2)	(3)	(4)	means
Beech	5.7	6.2	6.0	6.1	6.0
Buttercups	16.6	15.2	15.4	16.5	15.9
Crucifers	3.4	3.5	3.8	3.3	3.5
Heaths	17.5	16.8	17.4	17.0	17.2
Rosebay willow-herb	7.5	9.4	7.7	9.3	8.5
Sycamore	11.0	12.4	12.3	11.4	11.8
White clover	6.7	6.3	6.5	6.4	6.5

(Chromatographic separation)

TABLE 10.7

Pollen fructose (as % dry matter)

	Samples				
Pollen types	(1)	(2)	(3)	(4)	means
Beech	15.8	20.1	16.1	16.5	17.1
Buttercups	17.4	20.1	17.6	19.3	18.6
Crucifers	16.0	16.9	16.7	16.6	16.6
Heaths	28.2	24.3	24.7	22.1	24.8
Rosebay willow-herb	23.0	19.7	20.0	19.8	20.6
Sycamore	14.3	14.0	14.2	14.2	14.2
White clover	20.5	21.8	21.5	20.9	21.2

(Chromatographic separation)

TABLE 10.8

Pollen total sugars (as % dry matter)

	Samples				
Pollen types	(1)	(2)	(3)	(4)	means
Beech	31.2	23.7	28.0	24.1	26.8
Buttercups	31.4	39.3	33.4	38.6	35.7
Crucifers	21.4	24.5	22.5	21.2	22.4
Heaths	42.4	42.5	42.7	41.8	42.4
Rosebay willow-herb	35.8	36.7	36.0	36.6	36.3
Sycamore	24.9	30.7	27.6	25.3	27.1
White clover	27.1	29.8	29.7	27.5	28.5

(A total reducing sugars estimate was performed on a hydrolysed extract).

TABLE 10.9

Pollen free reducing sugars (as % dry matter)

	Samples				
Pollen types	(1)	(2)	(3)	(4)	means
Beech	22.5	32.2	22.9	24.5	25.5
Buttercups	37.9	27.8	33.3	31.9	32.7
Crucifers	23.8	20.2	22.1	22.4	22.1
Heaths	42.5	43.7	42.5	40.2	42.2
Rosebay willow-herb	35.6	30.7	30.6	31.8	32.2
Sycamore	29.2	22.7	24.9	25.7	25.6
White clover	28.9	23.9	27.2	24.6	26.2

TABLE 10.10

Pollen 'xylan' (as % dry matter)

	Samples				
Pollen type	1.	2.	3.	4.	means
Beech	3.4	3.6	3.7	3.4	3.5
Buttercups	15.0	15.4	15.2	15.3	15.2
Crucifers	4.2	3.2	4.0	3.9	3.8
Heaths	10.0	8.9	9.3	9.8	9.5
Rosebay willow-herb	9.3	9.6	9.5	9.5	9.5
Sycamore	4.2	3.7	4.1	3.9	4.0
White clover	5.4	4.5	5.3	4.9	5.0

TABLE 10.11

Pollen 'cellulose' (as % dry matter)

	Samples				
Pollen type	1.	2.	3.	4.	means
Beech	0.02	0.41	0.27	0.33	0.26
Buttercups	0.93	0.54	0.62	0.85	0.74
Crucifers	0.60	0.93	0.61	0.90	0.76
Heaths	0.12	0.22	0.17	0.19	0.18
Rosebay willow-herb	0.47	0.71	0.70	0.66	0.64
Sycamore	0.43	0.70	0.64	0.63	0.60
White clover	0.54	0.40	0.51	0.48	0.48

TABLE 10.12

Pollen 'lignin' (as % dry matter)

Pollen type	Samples 1.	2.	3.	4.	means
Beech	15.5	14.9	15.2	15.4	15.3
Buttercups	14.6	15.1	14.8	15.0	14.9
Crucifers	22.5	21.8	22.3	22.2	22.2
Heaths	10.5	11.1	10.9	10.8	10.8
Rosebay willow-herb	15.5	14.9	15.1	15.4	15.2
Sycamore	14.9	14.4	14.8	14.6	14.7
White clover	20.6	20.1	20.3	20.5	20.4

TABLE 10.13

The sodium content of pollen (as % dry matter)

Pollen type	Samples 1.	2.	3.	4.	means
Beech	0.032	0.007	0.005	0.008	0.013
Buttercups	0.064	0.048	0.015	0.013	0.035
Crucifers	0.071	0.051	0.007	0.009	0.035
Heaths	0.020	0.021	0.016	0.012	0.017
Rosebay willow-herb	0.015	0.011	0.006	0.027	0.013
Sycamore	0.015	0.035	0.013	0.021	0.021
White clover	0.009	0.013	0.010	0.011	0.011

TABLE 10.14

The manganese content of pollen (as ppm dry matter)

Pollen type	Samples 1.	2.	3.	4.	means
Beech	18	28	21	25	23
Buttercups	40	35	43	50	42
Crucifers	15	12	18	21	17
Heaths	215	200	217	203	209
Rosebay willow-herb	17	12	13	15	14
Sycamore	56	47	51	58	53
White clover	22	19	19	23	21

TABLE 10.15

The phosphorus content of pollen (as % dry matter)

Pollen type	Samples 1.	2.	3.	4.	means
Beech	0.39	0.29	0.34	0.37	0.35
Buttercups	0.52	0.44	0.46	0.50	0.48
Crucifers	0.52	0.50	0.53	0.49	0.51
Heaths	0.30	0.39	0.37	0.31	0.34
Rosebay willow-herb	0.28	0.40	0.37	0.29	0.34
Sycamore	0.51	0.50	0.52	0.53	0.51
White clover	0.45	0.42	0.44	0.42	0.18

TABLE 10.16

The calcium content of pollen (as % dry matter)

	Samples				
Pollen type	1.	2.	3.	4.	means
Beech	0.077	0.020	0.032	0.059	0.047
Buttercups	0.050	0.068	0.080	0.135	0.081
Crucifers	0.148	0.199	0.132	0.276	0.189
Heaths	0.143	0.131	0.186	0.244	0.176
Rosebay willow-herb	0.104	0.084	0.118	0.151	0.122
Sycamore	0.072	0.076	0.106	0.118	0.093
White clover	0.123	0.123	0.124	0.296	0.167

TABLE 10.17

The magnesium content of pollen (as % dry matter)

	Samples				
Pollen type	1.	2.	3.	4.	means
Beech	0.100	0.072	0.084	0.078	0.084
Buttercups	0.128	0.132	0.150	0.148	0.140
Crucifers	0.140	0.149	0.145	0.150	0.146
Heaths	0.077	0.077	0.088	0.075	0.079
Rosebay willow-herb	0.089	0.102	0.115	0.102	0.098
Sycamore	0.096	0.106	0.111	0.134	0.112
White clover	0.092	0.092	0.071	0.102	0.089

TABLE 10.18

The potassium content of pollen (as % dry matter)

Pollen type	Samples 1.	2.	3.	4.	means
Beech	2.25	0.52	0.51	0.61	0.97
Buttercups	1.80	1.56	0.68	0.80	1.21
Crucifers	1.58	2.45	0.64	0.67	1.34
Heaths	1.36	0.95	0.71	0.69	0.93
Rosebay willow-herb	1.34	1.11	1.02	0.87	1.04
Sycamore	0.92	1.90	0.84	0.97	1.16
White clover	0.85	0.91	0.62	0.87	0.81

TABLE 10.19

Amino acid analysis of 7 pollens (in duplicate : 9/16g N)

	Pollens													
	Beech		Buttercup		Crucifers		Heaths		Rosebay willow-herb		Sycamore		White clover	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Amino acids														
Aspartic acid	10.22	9.77	10.47	9.85	10.23	8.85	10.31	9.16	9.74	10.16	9.71	10.86	9.37	10.59
Threonine	5.22	4.44	5.80	5.21	5.25	4.56	5.15	4.11	5.32	4.56	4.60	4.65	4.33	4.63
Serine	5.37	4.74	6.33	5.88	5.88	5.10	5.56	4.89	6.28	5.82	5.14	4.88	4.92	5.17
Glutamic acid	12.54	12.11	2.84	10.86	11.98	10.41	12.45	9.42	10.38	11.21	11.01	12.36	10.95	12.78
Glycine	5.37	4.96	5.56	4.87	5.54	4.36	5.44	4.21	4.36	4.56	4.60	5.71	4.44	4.54
Alanine	5.22	4.89	5.39	4.42	5.25	4.93	5.39	5.00	5.26	5.93	4.68	6.11	4.84	5.61
Valine	6.12	5.94	5.92	5.38	5.47	4.26	6.20	4.58	5.26	5.22	5.32	6.15	5.32	5.17
Cystine	1.19	1.50	1.54	1.68	2.12	1.96	1.33	1.63	0.64	0.77	1.12	1.32	1.11	1.27
Methionine	2.09	1.95	2.54	2.74	2.23	2.03	1.62	2.11	1.92	2.75	2.01	2.26	2.14	2.24
Iso-leucine	4.70	4.81	4.91	4.87	4.80	3.95	5.27	3.63	4.17	4.45	4.35	5.58	4.44	4.58
Leucine	7.02	6.99	7.10	7.89	7.14	6.08	7.70	6.42	7.05	7.47	6.47	7.97	6.67	7.32
Tyrosine	3.36	3.46	3.91	3.64	3.39	2.57	3.65	2.89	3.40	3.63	3.42	3.95	3.45	3.51
Phenylalanine	4.55	5.64	4.85	4.59	4.61	3.58	4.86	3.84	3.85	5.00	4.39	5.02	4.33	4.68
Lysine	4.70	6.62	5.03	6.49	6.29	5.94	5.04	4.11	6.09	5.60	5.04	2.33	4.64	4.73
Histidine	1.79	2.26	1.72	2.02	2.01	1.82	2.26	1.68	3.21	3.96	1.65	1.86	1.98	2.00
Arginine	5.30	6.02	4.91	5.04	4.87	4.46	6.43	5.37	4.87	5.44	4.60	3.72	4.40	5.07
Totals	84.78	86.09	88.82	85.44	87.05	74.90	88.65	73.05	81.92	86.54	78.13	84.75	77.34	83.90

TABLE 10.20

Amino acid analysis of 4 honeybee carcasses (duplicate analyses: g/16g N)

Amino acids	Honeybees A		B		C		D	
	1	2	1	2	1	2	1	2
Aspartic acid	7.168	7.410	6.854	7.938	6.524	6.588	7.695	7.166
Threonine	3.514	3.765	3.373	3.604	3.537	3.564	3.728	3.718
Serine	4.424	4.515	4.121	4.397	4.231	4.077	4.224	4.276
Glutamic acid	9.912	11.415	10.350	9.904	10.441	11.165	10.346	9.565
Glycine	7.798	8.145	6.963	7.006	7.179	7.263	7.268	7.149
Alanine	8.260	8.865	7.290	7.157	6.956	6.791	7.986	7.504
Valine	6.090	6.285	5.834	5.531	5.751	5.724	6.259	5.949
Cystine	0.840	1.080	0.816	9.576	1.310	0.972	1.129	0.980
Methionine	1.344	1.305	1.238	1.247	1.245	1.350	1.368	1.420
Iso-leucine	4.718	4.785	4.298	4.637	4.520	4.860	4.976	4.766
Leucine	7.546	7.710	7.031	7.169	7.113	7.709	8.020	7.960
Tyrosine	3.962	3.735	3.400	3.465	3.773	4.388	3.146	4.293
Phenylalanine	2.884	3.150	2.870	3.238	3.576	3.267	3.129	3.312
Lysine	4.704	4.875	4.624	4.725	4.782	5.009	3.711	4.022
Histidine	2.324	2.370	2.230	2.129	2.214	2.484	1.984	2.349
Arginine	4.354	3.810	4.257	4.372	4.651	3.524	4.395	4.242
Total	79.842	83.215	75.548	77.477	77.801	78.732	79.361	78.670

TABLE 10.21

The Ca, Mg, K and Na content of honey from the North of Britain. (as ppm/volume)

Source		Ca	Mg	K	Na
Aberdeen	Deeside	70	-	1950	135
Angus	Dundee (1)	40	14.8	640	25
	Dundee (2)	184	40.8	1535	92
Argyll	(1)	184	26.4	750	32
	(2)	70	80.	4680	178
	(3)	-	20.	1950	61
Berwick	Cockburnspath	530	-	707	86
	Lauder	148	15.6	436	62
	Longformacus	192	57.6	2450	116
East Lothian	Birnieknowes	72	22.	850	40
	Danskine (1)	160	20.8	1620	43
	Danskine (2)	96	15.2	544	37
	Dunbar	-	20.0	3610	153
	East Linton (1)	184	24.8	1000	65
	East Linton (2)	104	10.0	249	48
	Gifford	160	28.8	1620	70
	Lammermuirs (1)	288	42.0	1810	96
	Lammermuirs (2)	196	38.0	1400	84
	Moreham (1)	144	38.0	800	70
	Moreham (2)	300	56.0	2450	109
	North Berwick (1)	140	30.8	1700	82
	North Berwick (2)	160	30.4	1840	74
	Nunraw	170	18.0	785	50

Source		Ca	Mg	K	Na
East Lothian	Pencaitland (1)	96	18.4	490	65
	Pencaitland (2)	144	17.6	735	41
	Prestonhall	128	28.8	1400	45
	Seacliff	96	31.2	657	44
	Whittingham	160	16.0	1250	34
Fife	Auchtermuchty	84	30.0	2250	153
	Falkland	52	19.6	780	44
	Freuchie	200	43.2	2330	126
	Wormit	104	20.8	825	49
Inverness	Carrbridge	88	20.0	1100	107
Lanark	Dolphington	284	44.8	2090	96
	Dunsyre (1)	184	24.0	1050	92
	Dunsyre (2)	116	16.0	448	70
	Symington (1)	240	24.8	1070	91
	Symington (2)	196	18.0	620	117
	Symington (3)	280	56.0	2000	108
Midlothian	Arniston (1)	160	24.0	860	65
	Arniston (2)	144	24.8	955	52
	Bush (1)	90	24.0	4400	40
	Bush (2)	208	40.0	2070	79
	Bush (3)	120	-	3630	76
	Bush (4)	90	15.0	4530	38
	Currie	260	29.6	1580	141
	Dalkeith	184	30.8	2000	35
	Dalmahoy	192	30.0	2070	50
	Dryden	116	24.0	2060	47

Source		Ca	Mg	K	Na
Midlothian	Edinburgh	64	21.0	2060	172
	Edinburgh - Craigleith	160	19.2	1160	37
	Edinburgh - Grange	184	24.8	1430	58
	Gorebridge (1)	144	24.8	810	58
	Gorebridge (2)	168	26.4	1140	64
	Lasswade	208	23.2	1400	44
	Musselburgh	52	23.6	739	66
	Pathhead	172	14.4	705	40
	Torsance	128	8.0	200	54
	Ratho	108	25.6	1675	136
Peebles	Broughton (1)	88	23.0	900	77
	Broughton (2)	52	9.2	365	63
	Elibank	176	160.0	3160	76
	Houndleshope (1)	268	27.2	1120	116
	Houndleshope (2)	260	38.4	1810	88
	Innerleithen - Kirkhouse	180	24.8	1270	60
	Innerleithen - The Glen(1)	240	32.8	1660	94
	The Glen(2)	296	44.8	2000	113
	Manor (1)	140	36.0	1650	112
	Manor (2)	224	23.2	1070	91
	Peebles	160	11.2	592	90
	Stobo	196	23.2	1150	75
Perth	Abernethy	52	14.8	685	45
	Auchterarder	68	21.6	875	67
	Birnam	192	64.0	2530	87

Source		Ca	Mg	K	Na
Perth	Blairgowrie	68	19.2	1020	73
	Errol	184	43.2	1785	34
	Forgandenny	68	20.4	850	68
	Forteviot	68	19.6	1890	59
	Glen Quaich	240	68.8	2925	83
Roxburgh	Kelso (1)	192	52.4	2375	96
	Kelso (2)	128	25.6	1400	46
	Morebattle	104	18.0	423	48
Selkirk	Caddonfoot	52	13.2	657	44
West Lothian	Dalmeny (1)	160	45.0	2500	82
	Dalmeny (2)	96	26.0	1325	54
	Kirkliston	140	22.4	1250	114
	Philipston	96	19.2	551	35
Scotland other than the Counties		60	-	1290	73
	Detailed above	-	-	360	55
		30	63.0	2740	66
		110	22.0	2050	88
		-	-	190	55
		140	70.0	2960	109
		82	-	1800	72
Northumberland	Horncliffe	160	42.8	1755	74
	Wooler (1)	128	26.0	540	55
	Wooler (2)	90	9.6	133	48

APPENDIX 11

Pollen sampling

Twenty samples of 1 g were taken from a pollen collection. On each occasion after speciating and weighing they were mixed back in the collection before another sample was taken. From these observations the composition of this pollen collection and the variation in the estimation of each pollen type was calculated (see Table 2.1). From this on a basis of a 20% coefficient of variation it would require a sample of 23 g for a 5% accuracy and one of 4 g for a 10% accuracy.

TABLE 11.1

Pollen types in the pollen collection

Pollen type	%	Coefficient of variation
Cruciferae	37	21.6
Chamaenerion angustifolium	32	13.0
Trifolium repens	24	21.0
Ericacae	5	36.2